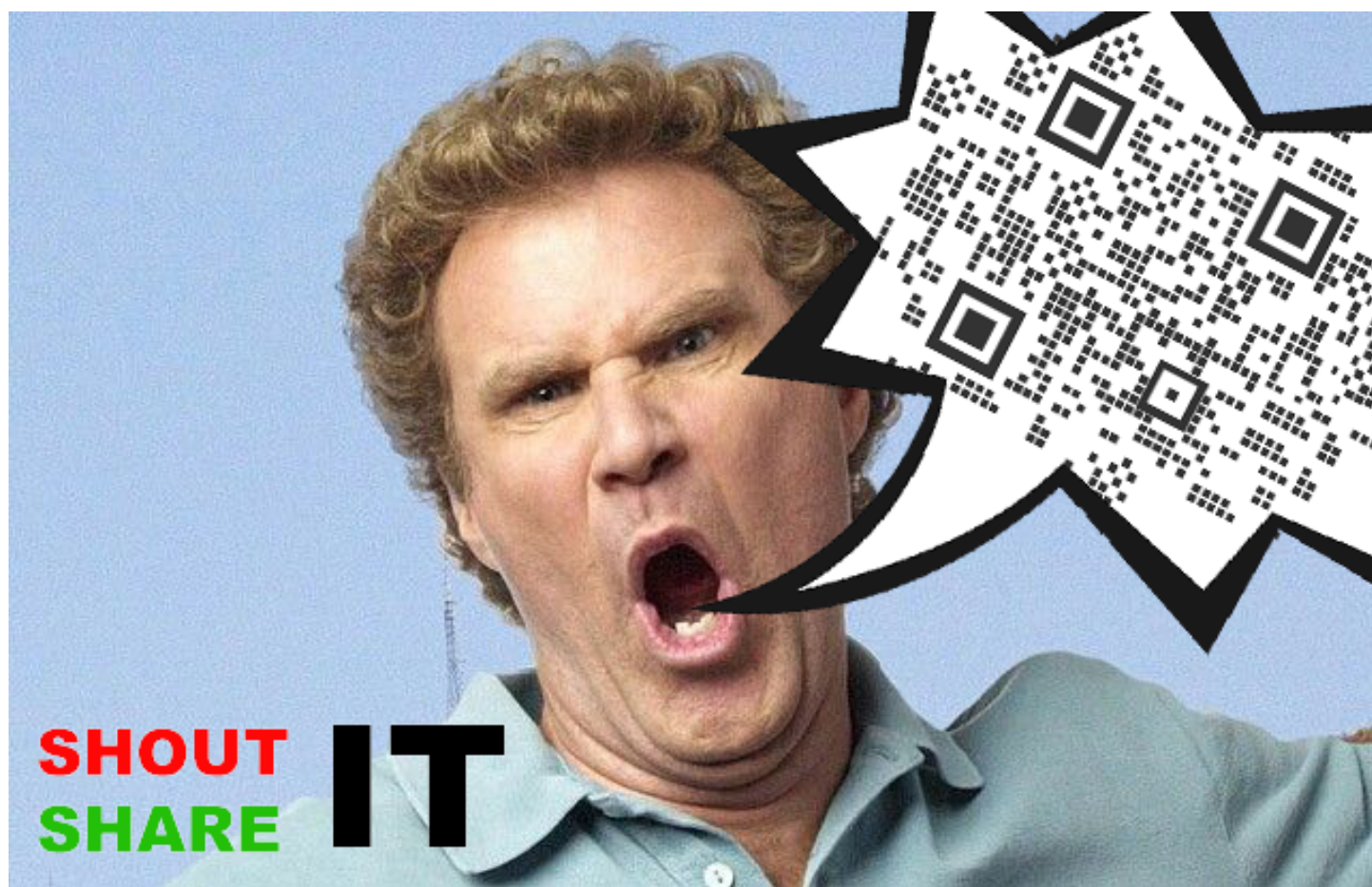




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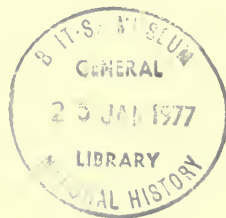
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A GUIDE TO THE SPECIES OF THE
GENUS *EUPLOTES*
(HYPOTRICHIDA, CILIATEA)



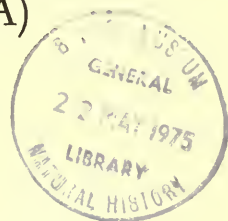
C. R. CURDS

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By COLIN R. CURDS

INTRODUCTION

ALTHOUGH species of the genus *Euplotes* Ehrenberg, 1830 are frequently observed in both marine and freshwater samples it is often not possible for the protozoologist to make specific identifications. This difficulty is due to at least three major factors ; firstly, many of the features used for distinguishing species within the genus are known to vary considerably even within clonal cultures, secondly, there is a large amount of confusion in the literature concerning the identity of certain common species and thirdly, there is the added difficulty of having to search through a considerable body of literature before an identification can be attempted. It is hoped that the present paper will help solve some of these problems by gathering together descriptions and diagrams of all those organisms considered to be distinct *Euplotes* species. Naturally the serious worker will still wish to refer to the original material but the volume of literature needed to be examined should be significantly reduced. The revisions of Tuffrau (1960) and more recently the species lists of Borror (1972) have been of considerable value but one is still left with the problem of searching through a large amount of original papers. Finally, to the author's knowledge no attempt has been made to devise a key to the species of *Euplotes* since that of Kahl (1932).

FEATURES OF TAXONOMIC IMPORTANCE

In the past 200 years over 80 species and varieties of the genus *Euplotes* have been described. Until relatively recently the species were separated simply on a basis of body size and shape, on the dorsal and ventral ridges and on the arrangement of the cirri on the ventral surface. Several decades were to pass after the introduction of the 'wet' silver impregnation method by Chatton and Lwoff (1930) before Tuffrau (1954) first discovered that the silver-line system or argyrome might be of taxonomic importance for species determination in the genus *Euplotes*. Tuffrau (1954) first suggested that the numbers of dorsolateral rows of cilia, the geometry of the argyrome, the number of frontoventral cirri and the form of the macronucleus could be used to distinguish species and later (Tuffrau, 1960) he presented his revision of the genus based on these ideas. Since that revision more species have been redescribed and confirmed on the basis of silver preparations (principally Borror 1962, 1963, 1968a) and several new species have been introduced. Borror (1972) published a list of species he found acceptable based on modern criteria together with their probable synonyms. In general the present author's findings confirm those of Borror (1972) although there are several instances where changes have been suggested. Carter (1972) added four new species to the list of Borror (1972) and redescribed seven others, furthermore he was able to suggest from his investigations

that the shape of the adoral zone of membranelles (AZM) and the number of membranelles therein were also useful additional features for separating species within the genus.

It is unfortunate that of the taxonomic characters mentioned above only one – the gross geometry of the dorsal argyrome – remains constant. All other features have been reported to vary to a greater or lesser extent and an account of some of these variations follows. However, the application of these modern criteria now makes it possible to examine and reappraise the species and varieties within the genus.

(a) *General morphological and ecological features*

Although Kahl (1932) used the habitat of *Euplotes* species as a strict taxonomic character he was ill advised to do so since several species are known to be euryhaline. However, specialized habitats such as the digestive tracts of sea urchins may be useful for species determination. To date only two species have been recorded in urchins, *E. balteatus* (Dujardin, 1841) which may be found both as a commensal and free-living and *E. tuffraui* Berger, 1965 which seems to be limited to a commensal mode of life. The size of a *Euplotes* species can be used as a taxonomic feature but must be applied with extreme caution. It is true that the smallest species never attain the size of the largest species and *vice versa* but it is also known that the size of a ciliate may vary with several parameters including its rate of growth (Curds, West and Dorahy, 1974), the concentration of food (Curds and Cockburn, 1971) and kind of food (Giese, 1938; Tuffrau, 1964). The overall shape of a *Euplotes* species is perhaps a rather more stable feature but is of limited taxonomic value since few species have really characteristic outline shapes.

Dorsal and ventral ridges are sometimes of value in species determination particularly when comparing modern preparations with early descriptions where ridges were often clearly figured. Borror (1968a) discussed cortical sculpturing and suggested that the use of nigrosin-HgCl₂-formalin method (Borror, 1968b) might help create a union of old and new species within the genus.

Coloured species of *Euplotes* have been encountered for many years; both Ehrenberg (1840) and Stein (1859) described green species which were likely to be forms of *E. patella* (Muller, 1773). Later Kahl (1932) listed three 'formae' of *E. patella* which contained zoochlorellae. It should be emphasized that one must distinguish between organisms feeding on green algae and those bearing zoochlorellae. Since Kahl (1932) only Diller and Kounaris (1966) seem to have mentioned zoochlorellae in *Euplotes*, and they described *E. daidaleos* Diller and Kounaris, 1966, a species closely related to *E. patella*, as continually containing zoochlorellae and this perhaps is the only valid record although it would be unwise to dismiss the observations of the early workers too readily.

(b) *Cirri*

The numbers and arrangement of the cirri on the ventral surface of *Euplotes* have been used as important taxonomic features for many years. Earlier workers

arrangement within a particular species. Most *Euplotes* possess 10 or 9 frontoventral cirri, far fewer have 8 while only *E. raikovi* Agamaliyev, 1966 has been reported to have 7 frontoventrals. With the exception of *E. tuffraui* the variation in frontoventral numbers seems to depend upon streak V (Wallengren, 1900 system, see Fig. 1). *Euplotes raikovi* was reported (Agamaliyev, 1967) to exhibit intraspecific polymorphism in the number of frontoventrals; he noted that there were 7 or 8 frontoventral cirri and indicated that cirrus V2 (Fig. 1) was that which did not develop in some specimens. Washburn and Borror (1972) described a strain of *E. raikovi* from America in which an eighth cirrus (V2) never developed although they did observe a barren plaque in each case. Curds (1974) recently reported a similar case in his description of *E. parkei* Curds, 1974 where cirrus V2 was present in some and absent from other specimens even within the same clone. The frontoventral cirri of *E. tuffraui* show a wider variation than reported in other species and furthermore the variation is not due to streak V but to streaks III and IV. Berger (1965) stated that the majority of *E. tuffraui* isolated from the digestive tracts of sea urchins possess 8 frontoventral cirri although he found 11 specimens that had 10 frontoventrals which was apparently due to the subdivision of the cirrus bases III 2, III 3 and IV 2. A further two specimens were found with 9 frontoventral cirri where only cirrus bases III 3 and IV 2 were subdivided. With the exception of the examples listed above the number and positioning of the frontoventral cirri nevertheless remain very valuable taxonomic characters that have been widely used in the past and will do so in the future.

(c) *The dorsal argyrome*

The overall geometrical pattern of the dorsal argyrome is one feature of taxonomic importance that, to date, has not been reported to vary. Tuffrau (1960) first introduced this feature for taxonomic purposes and he described three general types which he called 'musculicola', 'eurystomus' and 'vannus' after the species in which he first found them. Since that time many more silver-line systems of *Euplotes* species have been described in the literature and it is now possible to divide the dorsal argyrome patterns into five or six types as shown in Fig. 2.

The simplest type (Fig. 2a) includes six species whose dorsal interkinetal argyrome pattern is composed of longitudinal kineties with simple transverse connections between them so that there is a single row of polygons between the dorsal cilia or bristles. This group corresponds to the 'vannus' type of Tuffrau (1960) although it is suggested that the term 'single-vannus' is more descriptive and consistent with the terms to be used later.

The first complication in the dorsal argyrome pattern is shown in Fig. 2b, where the longitudinal rows of polygons are split centrally so that there are two longitudinal rows of polygons, approximately equal in width, between the rows of dorsal cilia. This group corresponds to some of those Tuffrau (1960) called the 'eurystomus' type although it would appear that the organism that this author identified as *E. eurystomus* (Wrzesniowski, 1870) was in fact *E. aediculatus* Pierson, 1943. However, since both of these species have dorsal argyromes of the same overall pattern and since 'eurystomus' type is now a widespread term it is suggested that it is kept but

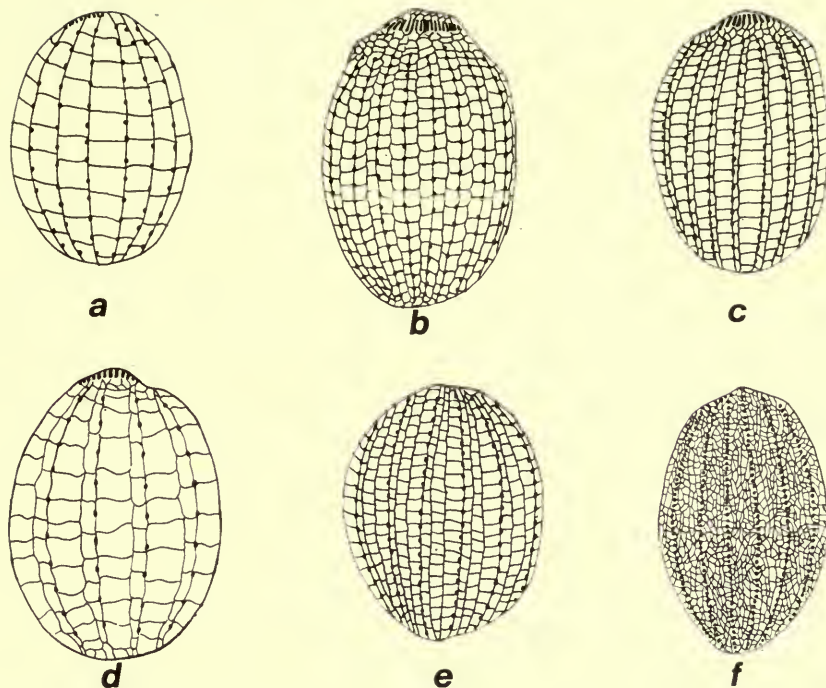


FIG. 2. Dorsal argyrome patterns of *Euplotes*. a. Single-vannus type. b. Double-eurystomus type. c-d. Double-patella types. e. Multiple type. f. Complex type.

expanded to 'double-eurystomus' type which will serve to distinguish that group of 24 species from another group of 8 species which also have double but unequal rows of polygons between the dorsal cilia. Perhaps the best known species in the latter group is *E. patella* (Muller, 1773) which Tuffrau (1960) included in his 'eurystomus' group and for this reason it is suggested that the pattern be called the 'double-patella' type. In this type the rows of polygons (Figs. 2c, 2d), between the dorsal cilia, are obviously unequal in width; in all but two species the wide rows of polygons are situated on the left of the rows of dorsal cilia (Fig. 2c), but in *E. strelkovi* and *E. zenkewitchi* Burkovsky, 1970 the wide rows are on the right and the narrow rows on the left of the kineties (Fig. 2d). It could be argued therefore that the 'double-patella' type should be further divided into these two sub-types, but this does not seem warranted unless more species whose argyrome patterns conform to the second sub-type are found.

In the present author's opinion the 'musculicola' type of Tuffrau (1960) included a heterogeneous assemblage of dorsal argyrome patterns that should now be divided into two more natural groups. It is therefore suggested that the term 'musculicola' type be discontinued and replaced by the terms 'multiple' type and 'complex' type. When the dorsal argyrome patterns of these two types are examined it can be seen that (Figs. 2e, 2f) the tendency for the rows of polygons to become further

subdivided is continued so that the next complication is that 3 or 4 regular rows of polygons of equal width may be found between the rows of dorsal cilia (Fig. 2e) and these conditions are found in *E. indentatus* Carter, 1972 and *E. muscicola* Kahl, 1932 respectively. It is suggested that argyrome patterns such as these be called 'multiple' types.

The final complication in dorsal argyrome patterns is that the polygons become so subdivided that an irregular network or mesh is formed between the dorsal cilia so that distinct rows of polygons cannot be distinguished. It is suggested that this pattern be called the 'complex' type (Fig. 2f). The latter pattern is illustrated well by the species *E. gracilis* Kahl, 1932, *E. muscorum* Dragesco, 1970 and *E. elegans* Kahl, 1932 but not so well by *E. moebiusi* the fourth member of the group. In *E. moebiusi* the dorsal argyrome consists of a mixture of well-defined regular polygons interspersed with an irregular meshwork.

With two exceptions the dorsal argyrome patterns of the species of *Euplotes* that have been described to date fit neatly into the types outlined above. One of these exceptions, *E. moebiusi* has already been mentioned and can readily be fitted into the 'complex' group by the presence of an irregular meshwork between the dorsal cilia. The other exception, *E. tegulatus* Tuffrau, 1960, which was previously placed in the 'eury stomus' type (Tuffrau, 1960) is more difficult since it could almost equally well be fitted into the 'double-eury stomus' or 'multiple' groups. In the case of *E. tegulatus* the dorsal argyrome pattern (see Fig. 46) consists of two longitudinal rows of large polygons between the dorsal cilia as in *E. eury stomus* but here there is also a central regular line of narrow elongate polygons. *Euplotes tegulatus* therefore displays what could be interpreted as an intermediate stage between the typical 'double-eury stomus' type and the typical 'multiple' type as shown in *E. indentatus*. In the author's opinion it seems more appropriate to place this species in the 'multiple' type group and reserve the 'double-eury stomus' type group solely for those species with two equal rows of polygons between the kineties.

Whereas the overall geometrical pattern of the dorsal argyrome appears to be a completely stable feature, the number of dorsolateral kineties has been reported to vary in several species including the following; *E. polycarinatus* Carter, 1972 (20-21 kineties), *E. variabilis* Stokes, 1887 (a synonym of *E. eury stomus* Kahl, 1932, 8-12 kineties), *E. eury stomus* (a synonym of *E. aediculatus*, 8-9 kineties) (see Carter, 1972, for all three species), *E. vannus* (8-9 kineties, see Heckmann, 1963), *E. mutabilis* Tuffrau, 1960 (11-13 kineties, see Tuffrau, 1960), *E. eury stomus* (8-9 kineties, see Bonner, 1954) and *E. tuffraui* (9-10 kineties, see Berger, 1965). However, in the majority of species the number of dorsolateral kineties remains constant. In the case of *E. mutabilis*, Tuffrau (1960) concluded that the variation in the number of kineties was accidental and exceptional, although even accidental variations seem to be widespread in nature. In single clonal cultures Bonner (1954), Carter (1972) and Heckmann (1963) have all reported instances of variation in the number of dorsolateral kineties. Furthermore, Carter (1972) found in three strains of *E. eury stomus* (a synonym of *E. aediculatus*) that the number of kineties was constant within the clone but different from clone to clone. In spite of variations such as these the number of kineties in most cases is a good reliable taxonomic character.

The numbers of kinetosomes or dorsal cilia plaques are more variable than those of kineties, even so variation within the clone is frequently much less than from species to species. Although several authors have recorded the number of dorsal cilia and by doing so have inferred that they are of taxonomic value no one has yet suggested this number to be of real taxonomic importance. In the key that follows the number of dorsal cilia has been used frequently but only when the numbers are sufficiently different to warrant their use. In each case the approximate range in the mid-dorsal kineties (where they are most numerous) are given.

(d) *The ventral argyrome*

The gross geometry of the ventral argyrome is of little taxonomic value since distinctive patterns are not immediately recognizable. However, some authors have used the general size of the constituent polygons on a comparative basis and this may be given as additional information. Silver-line preparations of the ventral surface display the infraciliary network, the cirri plaques and the adoral zone of membranelles (AZM) which is of kinetosomal origin. Whereas in the past the size and shape of the AZM have often been used as taxonomic features, the number of membranelles therein has only recently been introduced. Carter (1972) found, in 11 species that he studied, that the AZM features were even more stable than those characters suggested by Tuffrau (1960). However, all the features of the AZM are known to vary and the classic example is that of *E. balteatus* which exhibits polymorphism depending upon the nature of the food supply. Tuffrau (1964) found that both the size and shape of the AZM of *E. balteatus* was dependent upon the size of the cell and the number of membranelles in the AZM varied from 25 to 30 in small cells and from 70 to 80 membranelles in the case of giant individuals. Fortunately variation of this magnitude seems to be confined to that species, nevertheless variation in the number of membranelles is commonly observed. For this reason the approximate ranges of membranelle numbers are given and their use has been restricted to cases when there is a considerable difference in the numbers between two species, for example when distinguishing *E. minuta* Yocum, 1930 (30–40 membranelles) from *E. vannus* (60–70 membranelles).

(e) *Nuclear features*

The protozoan nucleus has been used as an important diagnostic character in taxonomic schemes for many years and the dimorphic nuclei of ciliates have played an important part in ciliate taxonomy. The macronucleus of *Euplotes* is elongate and takes a variety of shapes which differ from species to species. Perhaps the most common form is the simple inverted C-shape while in others this has become modified to a 3-shape and in others the arms close to form a hoop- or horseshoe-like structure. In addition, several rather more bizarre forms are known. The micronucleus is usually small and round but it does vary in size and shape and in *E. tegulatus* and *E. aberrans* Dragesco, 1960 the micronucleus is particularly large.

The use of the shape of the macronucleus as a diagnostic feature in the genus *Euplotes* has been the subject of discussion for several years. Tuffrau (1960) supported the view that the nuclear features were of great taxonomic importance

provided the shape of the macronucleus was determined when in a 'quiescent state', that is to say when neither division nor conjugation is in progress. It is true to say that the macronucleus of *Euplotes* takes a variety of forms during reorganization and division and it is likely that these phenomena have been responsible for the confusion that has appeared in the literature. Nevertheless, the consensus of opinion seems to be that if the process of reorganization is understood and provided it is possible for the taxonomist to recognize the interphase macronucleus from one that is in another divisional state, then the interphase macronucleus is constant and characteristic of the species. The interphase macronucleus can be recognized by the presence of replication bands (Gall, 1959; Kluss, 1962; Prescott, Kimball and Carrier, 1962) which represent bands of DNA synthesis travelling from the two nuclear extremities towards the centre of the macronucleus. Prescott *et al.* (1962) showed that the macronucleus of *E. eurystomus* is in interphase when the replication bands are present along the macronuclear arms from tips to half the distance to the centre.

KEY TO THE GENUS *EUPLOTES*

It is unfortunate that silver-line preparations have not yet been made and described for all species of *Euplotes*. The key that follows relies heavily upon features displayed by the silver-line technique but a series of descriptions of undesignated species follows the key (Section F, p. 50) and this includes all those species whose silver-line systems have not yet been described. Diagrams of silver preparations are given for all species where available and these have been obtained directly from original descriptions. Unless otherwise specified all scales given on diagrams indicate 10 μ m. The characters for the key were selected and used in order of least variation. Therefore the first division of species into groups is made on a basis of the overall pattern of the dorsal argyrome and further subdivisions are made using the number of frontoventral cirri and dorsolateral kineties. Wherever possible, reported variations of a feature within a species has been taken into account; thus it is possible to identify *E. mutabilis* when it has a 'single-vannus' type argyrome or when undergoing reorganization and therefore appears to have a complex argyrome. Similarly it should be possible to identify *E. eurystomus* when it has any of the reported numbers of dorsolateral kineties and so on.

KEY TO THE MAJOR GROUPS OF SPECIES

- 1 a Single-vannus type dorsal argyrome (Fig. 2a) with single row of polygons between kineties 5 (Section A, p. 11)
- b Some other type of dorsal argyrome 2
- 2 a Double dorsal argyrome (Figs. 2b, 2c, 2d) with two rows of polygons between kineties 3
- b Multiple or complex dorsal argyrome (Figs. 2e, 2f) 4
- 3 a Double-eurystomus type dorsal argyrome (Fig. 2b) with two rows of equal-sized polygons between kineties 10 (Section B, p. 16)
- b Double-patella type dorsal argyrome (Figs. 2c, 2d) with alternate rows of wide and narrow polygons between kineties 36 (Section C, p. 38)

- 4 a Multiple type dorsal argyrome (Fig. 2e) with several (more than two) regular rows of polygons between kineties 43 (Section D, p. 45)
 b Complex type dorsal argyrome (Fig. 2f) with irregular meshwork of small polygons between kineties 45 (Section E, p. 47)

SECTION A. KEY TO SPECIES WITH A SINGLE-VANNUS TYPE DORSAL ARGYROME

- 5 a 8 or less dorsolateral kineties 6
 b 9 or more dorsolateral kineties 7
 6 a 6 dorsolateral kineties with 7-10 dorsal cilia in central rows *E. balticus*
 b 8 dorsolateral kineties with 11-15 dorsal cilia in central rows *E. cristatus*
 7 a 9 dorsolateral kineties 8
 b 10 or more dorsolateral kineties 9
 8 a About 22 dorsal cilia in central kineties and 60-70 membranelles in AZM *E. vannus*
 b About 13 dorsal cilia in central kineties and 30-40 membranelles in AZM *E. minuta*
 9 a 10 dorsolateral kineties with 26-30 dorsal cilia in central rows *E. crassus*
 b 11 dorsolateral kineties with 11-15 dorsal cilia in central kineties *E. mutabilis*

SECTION A. DESCRIPTIONS OF SPECIES

Euplotes balticus (Kahl, 1932) Dragesco, 1966

Kahl (1932) first described this species as *E. vannus* var. *balticus* while later Tuffrau (1960) considered it to be a synonym of *E. crassus*. However, the silver preparations of Dragesco (1966) make it clear that *E. balticus* is a distinct species.

DIAGNOSIS. *Euplotes balticus* (Fig. 3) is a medium-sized (60-100 μ m long) ovoid marine species. The peristome is long and narrow extending down to about $\frac{4}{5}$ of the body length with the AZM containing about 50 membranelles. There are 10 frontoventral, 5 transverse and 4 or 5 caudal cirri. The ventral argyrome consists of a few very large irregular polygons. The dorsal argyrome is of the single-vannus type with 6 dorsolateral kineties carrying about 10 dorsal cilia in the central rows. The macronucleus is C-shaped with a club-like extension on the posterior arm (Fig. 3b). The micronucleus is situated in a depression of the left anterior edge of the macronucleus. The contractile vacuole may have several satellite vacuoles surrounding it.

Euplotes crassus (Dujardin, 1841) Kahl, 1932

This species was first described by Dujardin (1841) under the name *Ploesconia crassa* Dujardin, 1841. Kahl (1932) noted that *E. violaceus* Kahl, 1928 was in retrospect a synonym of *E. crassus*. The silver-line system was first studied by Chatton and Séguela (1940) and fully described by Tuffrau (1960).

DIAGNOSIS. *Euplotes crassus* (Fig. 4) is a large (100-130 μ m long) elongate oval marine species. The dorsal surface is strongly sculptured by 8 longitudinal ridges. The peristome is long and narrow while the AZM consists of about 50 membranelles and extends $\frac{2}{3}$ down the body length. The dorsal argyrome is essentially simple of the single type and there are 10 dorsolateral kineties with the central ones bearing about 26 dorsal cilia. There are 10 frontoventral, 5 transverse and 5 or 6 caudal cirri. The macronucleus is C-shaped with the posterior arm bearing a foot-like

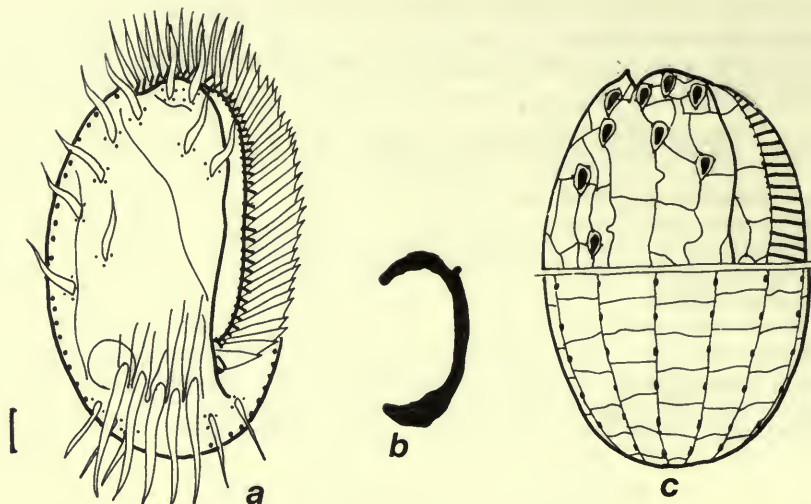


FIG. 3. *Euplotes balticus*. a. Ventral aspect. b. Nuclei. c. Ventral and dorsal argyrome patterns. (After Dragesco, 1966.)

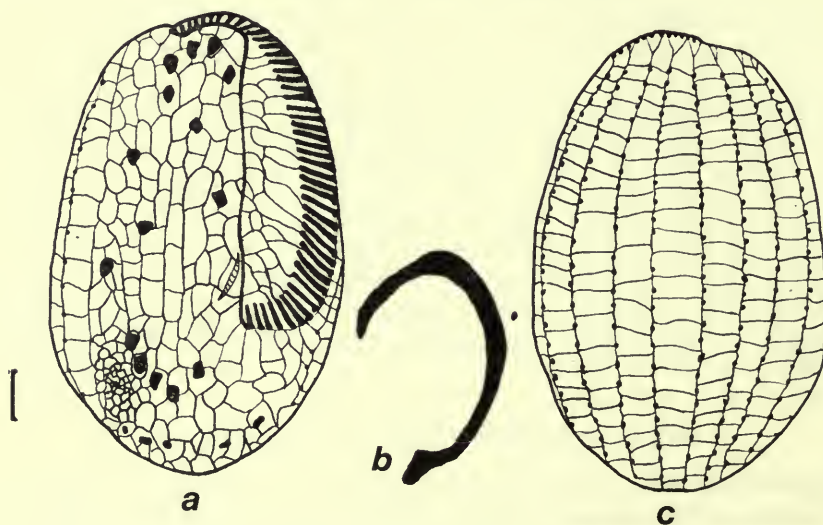


FIG. 4. *Euplotes crassus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

extension. The compact micronucleus is situated anteriorly near the left edge of the macronucleus.

Euplotes cristatus Kahl, 1932

This species was originally briefly described by Kahl (1932) and subsequently by Tuffrau (1960) and Carter (1972).

DIAGNOSIS. *Euplotes cristatus* (Fig. 5) is a medium (60 μm long, 45 μm wide) oval marine species. The buccal cavity is narrow and almost covered completely anteriorly by the lateral edge of the peristomial lip. The AZM is evenly curved, extends $\frac{1}{2}$ – $\frac{2}{3}$ of the length of the body and is composed of 35–47 membranelles. The dorsal surface is convex and there are 6 prominent ridges. The dorsal argyrome is of a simple single type with 8 dorsolateral kineties bearing 11–15 dorsal cilia in the central rows. There are 10 frontoventral, 5 transverse and 4 caudal cirri. In the original description Kahl (1932) noted the presence of only 3 caudal cirri whereas Tuffrau (1960) and Carter (1972) both found 4 caudals. The macronucleus is C-shaped with a heel-like extension on the posterior arm. The small, compact micronucleus is situated on the upper left border of the macronucleus.

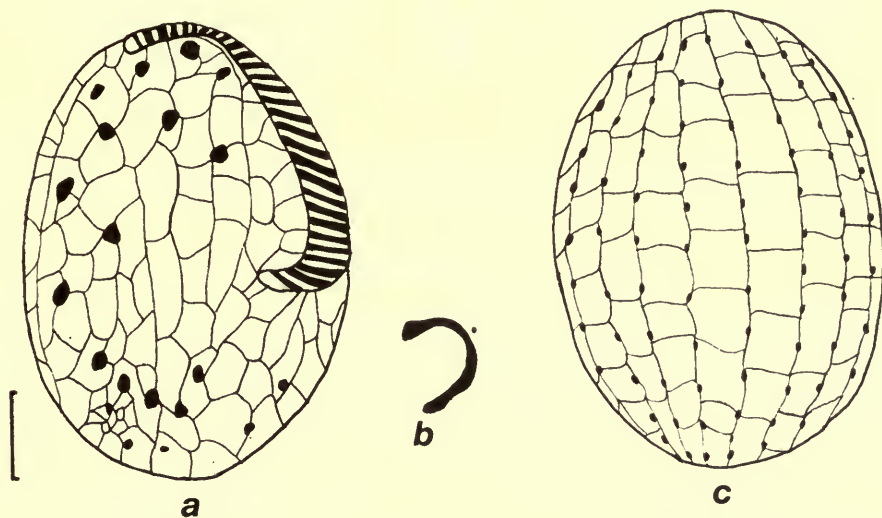


Fig 5. *Euplotes cristatus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

Euplotes minuta Yocum, 1930

Since the original description of *E. minuta* by Yocum (1930) this species disappeared into obscurity until Borror (1962) rediscovered it and described its silver-line system and general morphology.

DIAGNOSIS. *Euplotes minuta* (Fig. 6) is a small (54 μm long, 28 μm wide) oval marine species. The right margin of the peristome is almost straight and extends $\frac{3}{4}$ down the length of the body. The AZM consists of 30–40 membranelles. The dorsal argyrome is of the single type with 9 dorsolateral kineties bearing 12–13 cilia in the central dorsal rows. There are 10 frontoventral, 5 transverse and 4 caudal cirri. The macronucleus is C-shaped with the posterior arm carrying a knob on its left side and a foot-like extension (Fig. 6). The micronucleus is situated anteriorly on the left edge of the macronucleus.

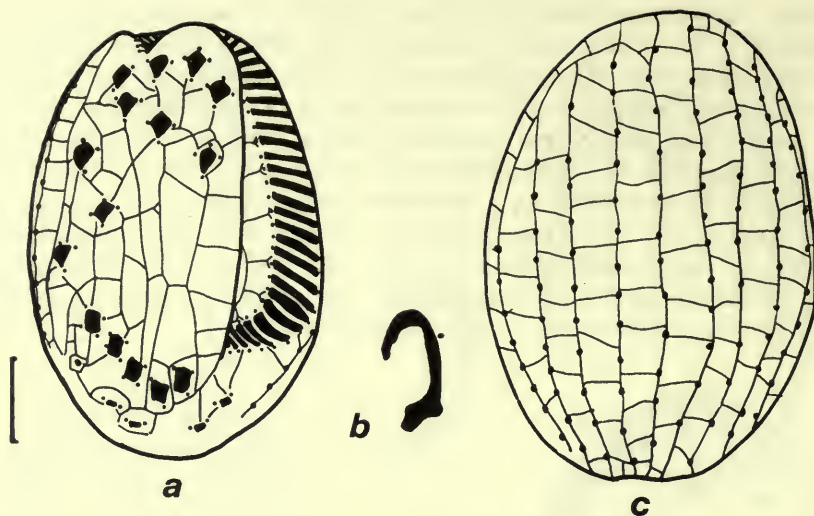


FIG. 6. *Euplotes minuta*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Borror, 1962.)

Euplotes mutabilis Tuffrau, 1960

This species was first found and described by Tuffrau (1960) in his revisionary monograph. Although the dorsal argyrome is of the single type, Tuffrau (1960) generally observed it as is shown in Fig. 7 where reorganization of the kinetosomal network is in progress. Tuffrau (1960) rarely found specimens in the quiescent state which he believed was due to the rapid growth rate of the population that he studied. This species has therefore been included in both single-vannus and complex sections of the key since it would depend on the state of the organism into which group it would appear to fall.

DIAGNOSIS. *Euplotes mutabilis* (Fig. 7) is a medium (95 μm long) oval marine species that is widest at its posterior extremity. The peristome is quite large and the right margin extends unevenly down the body to terminate in a spike-like projection. The AZM contains about 60 membranelles which extend down almost $\frac{3}{4}$ of the body length. The dorsal argyrome is single in the quiescent state but with several irregular ramifications when undergoing reorganization. There are 11 dorso-lateral kineties which bear 12 or 13 dorsal cilia in the central rows. There are 10 frontoventral, 5 transverse and 4 or 5 caudal cirri. The macronucleus is C-shaped with a pointed foot-like structure at the end of the posterior arm. The micronucleus is situated anteriorly.

Euplotes vannus (Muller, 1786) Minkjewicz, 1901

This species has a long history which is given in detail by Tuffrau (1960), and the list of synonyms in Appendix I is indicative of the problems that have arisen in the

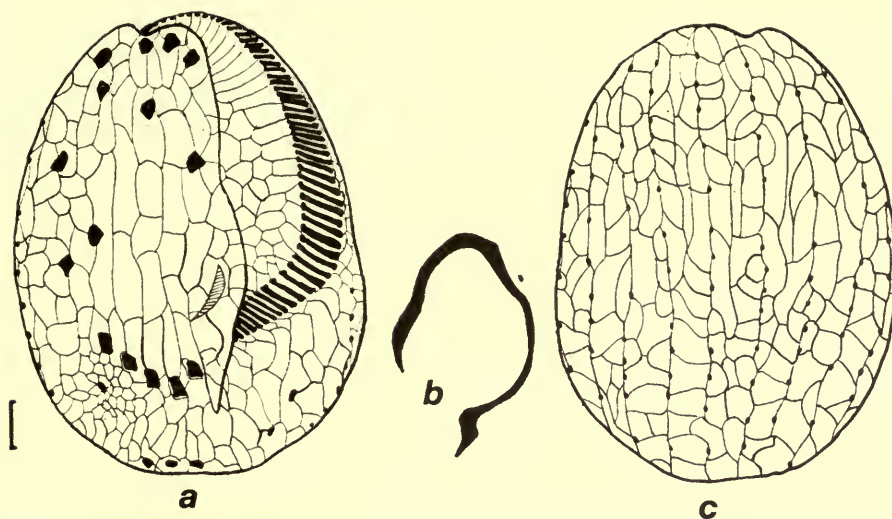


FIG. 7. *Euplotes mutabilis*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome in state of reorganization. (After Tuffrau, 1960.)

past but with the description of the silver-line system by Tuffrau (1960) most of the identification difficulties were eradicated.

DIAGNOSIS. *Euplotes vannus* (Fig. 8) is a medium-sized (75–100 μm long) marine species. It has an overall oval configuration but is slightly curved towards the right. The peristome is narrow but large and the AZM which extends $\frac{2}{3}$ down the length of the body contains over 60 membranelles. The dorsal argyrome is of the single type

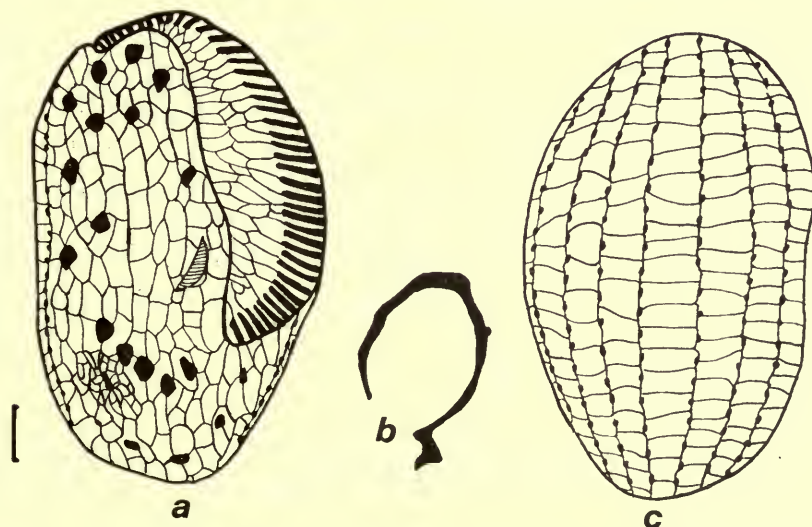


FIG. 8. *Euplotes vannus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

with 9 dorsolateral kineties carrying about 22 cilia in the central dorsal rows. There are 10 strong frontoventral, 5 transverse and 4 fine but rigid caudal cirri. The macronucleus is an open C-shape with a twisted foot-like extension to the posterior arm. The micronucleus is compact and lies close to and sometimes overlapping the macronucleus.

SECTION B. KEY TO SPECIES WITH A DOUBLE-EURYSTOMUS TYPE DORSAL ARGYROME

- | | | |
|------|--|----------------------------|
| 10 a | 6 or 7 dorsolateral kineties | 11 |
| b | 8 or more dorsolateral kineties | 16 |
| 11 a | 6 dorsolateral kineties | <i>E. latus</i> |
| b | 7 dorsolateral kineties | 12 |
| 12 a | Less than 10 dorsal cilia in central kineties | <i>E. affinis</i> |
| b | More than 11 dorsal cilia in central kineties | 13 |
| 13 a | 10 frontoventral cirri | 14 |
| b | 8 or 9 frontoventral cirri | 15 |
| 14 a | 3 caudal cirri, AZM with about 40 membranelles | <i>E. octocirratius</i> |
| b | 4 caudal cirri, AZM with about 20 membranelles | <i>E. trisulcatus</i> |
| 15 a | 8 frontoventral cirri | <i>E. poljanskyi</i> |
| b | 9 frontoventral cirri | <i>E. dogieli</i> |
| 16 a | 8 dorsolateral kineties | 17 |
| b | 9 or more dorsolateral kineties | 25 |
| 17 a | 10 frontoventral cirri | 18 |
| b | 9 or less frontoventral cirri | 22 |
| 18 a | Macronucleus C- or 3-shaped | 19 |
| b | Macronucleus hoop- or horseshoe-shaped | 21 |
| 19 a | Slim species, macronucleus 3-shaped | <i>E. antarcticus</i> |
| b | Ovoid species, macronucleus C-shaped | 20 |
| 20 a | 11-15 dorsal cilia in central kineties | <i>E. alatus</i> |
| b | 21-25 dorsal cilia in central kineties | <i>E. crenosus</i> |
| 21 a | Freshwater, 45-55 membranelles in AZM, extra-large cirri bases, 13-17 dorsal cilia in central kineties | <i>E. magnicirratius</i> |
| b | Marine or in sea urchins, two forms - a small one with 25-30 and a large one with 70-80 membranelles in AZM, 8-11 dorsal cilia in central kineties | <i>E. balteatus</i> |
| 22 a | 6-10 dorsal cilia in central kineties | 23 |
| b | 16-35 dorsal cilia in central kineties | 24 |
| 23 a | 8 frontoventral cirri (sometimes 9), 4 caudals and 10 dorsal cilia in central kineties | <i>E. parkei</i> |
| b | 9 frontoventral cirri, 3 caudals and 6 dorsal cilia in central kineties | <i>E. bisulcatus</i> |
| 24 a | Macronucleus flat-backed C-shape with micronucleus distinctly separate. AZM straight | <i>E. aediculatus</i> |
| b | Macronucleus 3-shaped with micronucleus within a cleft of it. AZM sigmoidal | <i>E. eurystomus</i> |
| 25 a | 9 dorsolateral kineties | 26 |
| b | 10 or more dorsolateral kineties | 38 |
| 26 a | Commensal in echinoids | <i>E. tuffraui</i> |
| b | Free-living | 27 |
| 27 a | 10 frontoventral cirri, AZM with 25-30 membranelles | <i>E. quinquecarinatus</i> |
| b | 9 frontoventral cirri, sigmoidal AZM with 46-65 membranelles | <i>E. eurystomus</i> |
| 28 a | 9 frontoventral cirri | 29 |
| b | 10 frontoventral cirri | 31 |
| 29 a | Commensal in echinoids, macronucleus C-shaped | <i>E. tuffraui</i> |
| b | Free-living, 3-shaped macronucleus | 30 |

30	a	10-12 dorsolateral kineties	<i>E. eurystomus</i>
	b	14 dorsolateral kineties	<i>E. amieti</i>
31	a	10 dorsolateral kineties	32
	b	11 or more dorsolateral kineties	33
32	a	7-15 dorsal cilia in central kineties, commensal in echinoids	<i>E. tuffraui</i>
	b	21-25 dorsal cilia in central kineties, free-living	<i>E. inkystans</i>
33	a	11 or 12 dorsolateral kineties	34
	b	13 or more dorsolateral kineties	35
34	a	11 dorsolateral kineties with about 18 dorsal cilia in central rows and 4 caudal cirri	<i>E. neapolitanus</i>
	b	12 dorsolateral kineties with up to 40 (rarely 18-21) cilia in central rows and 5-8 caudal cirri	<i>E. charon</i>
35	a	13 dorsolateral kineties with 36-42 dorsal cilia in central rows	<i>E. harpa</i>
	b	20-21 dorsolateral kineties with 20-23 dorsal cilia in central rows	<i>E. polycarinatus</i>

SECTION B. DESCRIPTIONS OF SPECIES

Euplotes aediculatus Pierson, 1943

Euplotes aediculatus was first described by Pierson (1943). Later both Tuffrau (1960) and Carter (1972) described organisms which were obviously *E. aediculatus* but named them *E. eurystomus*. Pierson, Gierke and Fisher (1968) produced well-documented evidence (Figs. 9, 10) on the differences between these two species.

DIAGNOSIS. *Euplotes aediculatus* (Figs. 9, 10) is a large freshwater hypotrich 105-160 μm long. The peristome is medium sized, triangular and has two depressions in the median border. One depression is located anteriorly whilst the other is more prominent and is situated midway along the peristomial border. The AZM collar is not as prominent as in *E. eurystomus*, is straight to curved but never sigmoidal

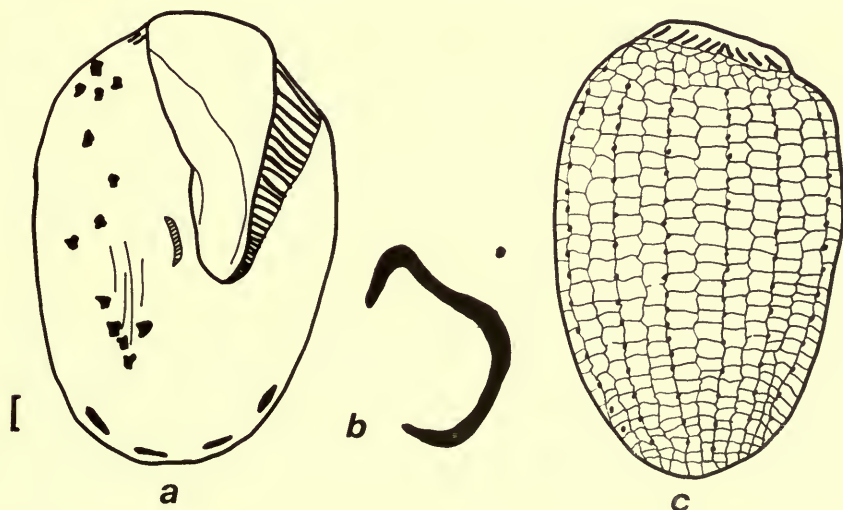


FIG. 9. *Euplotes aediculatus*. a. Ventral cirri. b. Nuclei. c. Dorsal argyrome.
(After Pierson, Gierke & Fisher, 1968.)

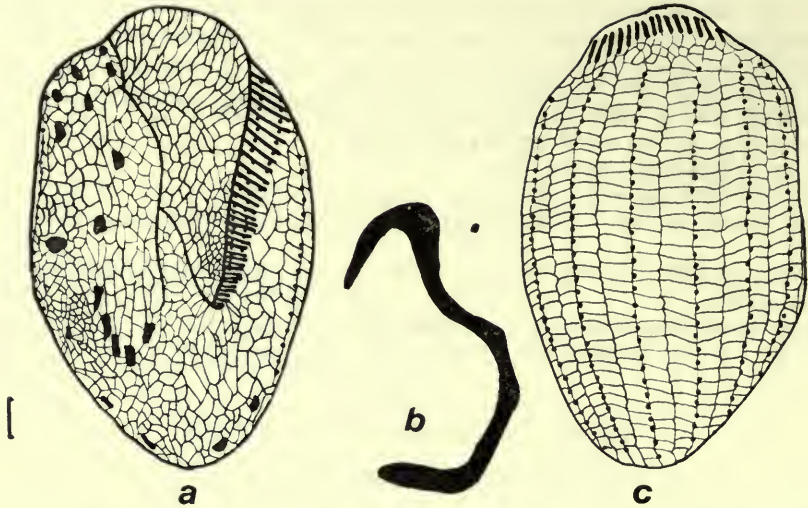


FIG. 10. *Euplotes aediculatus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

and contains about 40 membranelles. The macronucleus is C-shaped with an arched or flattened back and the micronucleus is distinctly separate from the macronucleus.

The dorsal argyrome is of the double-eurystomus type and there are typically 8 dorsolateral kineties with about 20 cilia in the central kineties on the dorsal surface. There are 9 frontoventral, 5 transverse and 4 caudal cirri.

Euplotes affinis (Dujardin, 1841) Kahl, 1932

Until recently *E. affinis* and its variety with three caudal cirri, *E. affinis* forma *tricirratus* Kahl, 1932 had not been described using modern techniques. Curds (1974) redescribed a freshwater species which closely resembles the latter form and gave diagrams of the silver-line system. Tuffrau (1960) considered *E. affinis* to be a synonym of *E. charon* (Muller, 1773).

DIAGNOSIS. *Euplotes affinis* (Fig. 11) is a small (38 μm long, 26 μm wide) ovoid freshwater hypotrich with 9 frontoventral, 5 transverse and 3-4 caudal cirri. One of the caudal cirri is larger than the others and is held stiffly out to the right. The ventral surface is sculptured with 3 prominent ridges and the dorsal surface with 5 longitudinal ridges. The AZM has 18-20 membranelles and extends $\frac{2}{3}$ the length of the cell. There is a small undulating membrane. The dorsal argyrome is of the double-eurystomus type with 7 dorsolateral kineties and a maximum of 9 dorsal cilia in the central kineties. The macronucleus is a definite 3-shape and there is a small compact anterior micronucleus.

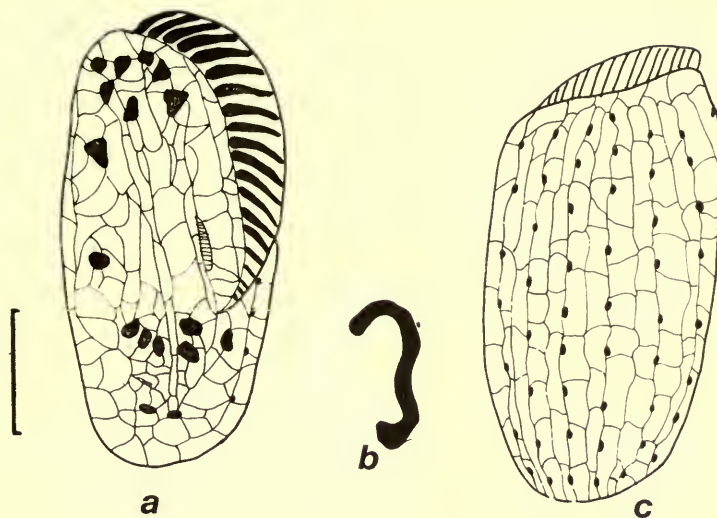


FIG. 11. *Euplotes affinis*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Curds, 1974.)

Euplotes alatus Kahl, 1932

The original description of this species was given by Kahl (1932) and new data concerning the silver-line system were added by Borror (1968a).

DIAGNOSIS. *Euplotes alatus* (Fig. 12) is a small (40 μm long, 30 μm wide) oval marine species. The dorsal surface has several inconspicuous low ridges but those on the ventral surface are far more conspicuous. The AZM extends just halfway down the length of the body and is composed of approximately 26 membranelles. The dorsal argyrome is of the double-eurystomus type with 8 dorsolateral kineties bearing 10–12 dorsal cilia in the central rows. There are 10 frontoventral, 5 transverse and 4–5 caudal cirri. The macronucleus is C-shaped which has an indentation in the left anterior edge which contains the small compact micronucleus.

Euplotes amieti Dragesco, 1970

This species is one of those described by Dragesco (1970) from the Cameroun in Africa. It has many similarities with *E. eurystomus* including the presence of a anterior peristomial pouch, a similar nucleus, a sigmoidal AZM which makes the present author doubt whether this is a true species or simply a geographical variety of *E. eurystomus*. However, because of the very large size, and more particularly the presence of 14 dorsolateral kineties, this organism has been treated here as a separate species until more information concerning *E. eurystomus* and *E. amieti* has been gathered.

DIAGNOSIS. *Euplotes amieti* (Figs. 13, 14) is one of the largest (140–240 μm long, 80–160 μm wide) species of *Euplotes* so far recorded. It is found in fresh waters

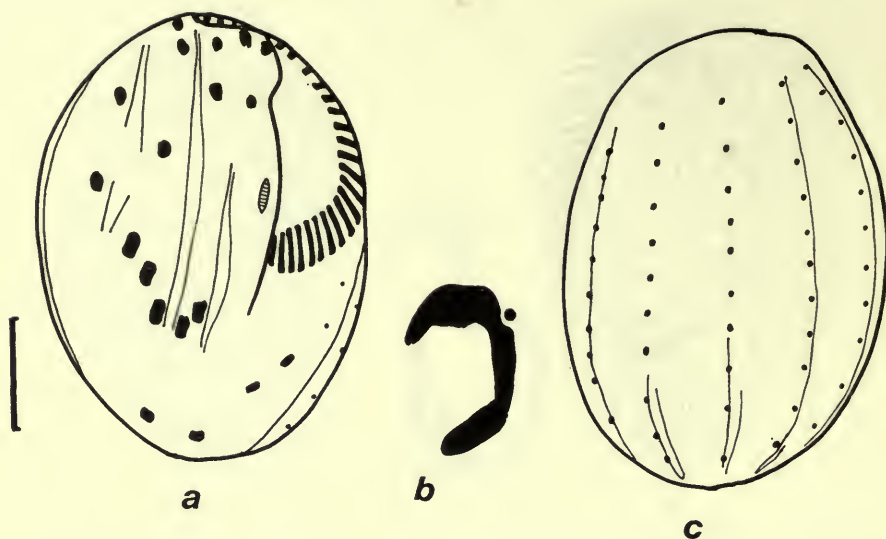


FIG. 12. *Euplotes alatus*. a. Ventral aspect. b. Nuclei. c. Dorsal aspect. (After Borror, 1968a.)

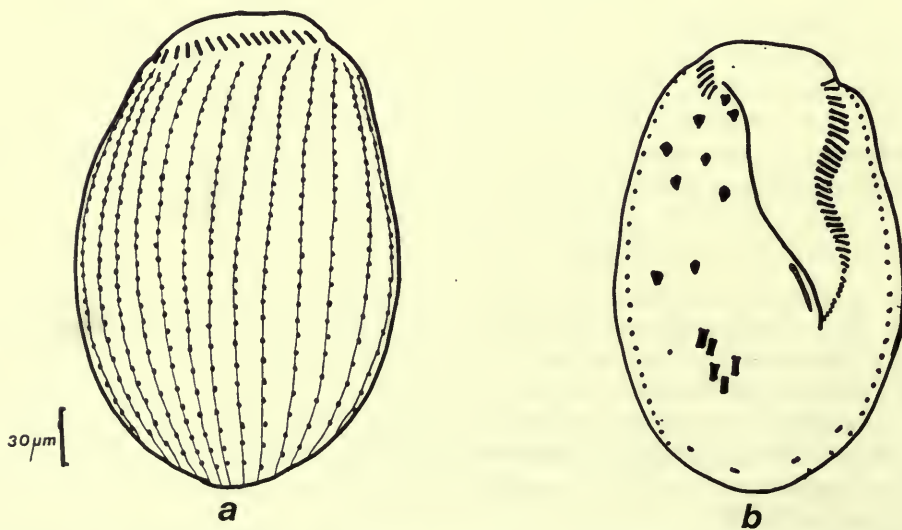


FIG. 13. *Euplotes amieti*. a. Dorsal aspect showing kinetids. b. Ventral aspect. (After Dragesco, 1970.)

and has a characteristic shape; the dorsal surface being highly convex while the ventral aspect is concave. The peristome is large, open and triangular in appearance. There is a well-developed peristomial collar and anterior pouch present. The AZM consists of 52-62 membranelles and winds sigmoidally down towards the cytostome. The dorsal argyrome is of the double-eurystomus type with 14 dorsolateral kineties bearing 28-30 cilia in the mid-dorsal rows. There are 9 frontoventral, 5 transverse and 4 caudal cirri. The macronucleus is an irregular 3-shape with a compact micronucleus situated in the left anterior corner of the macronucleus.

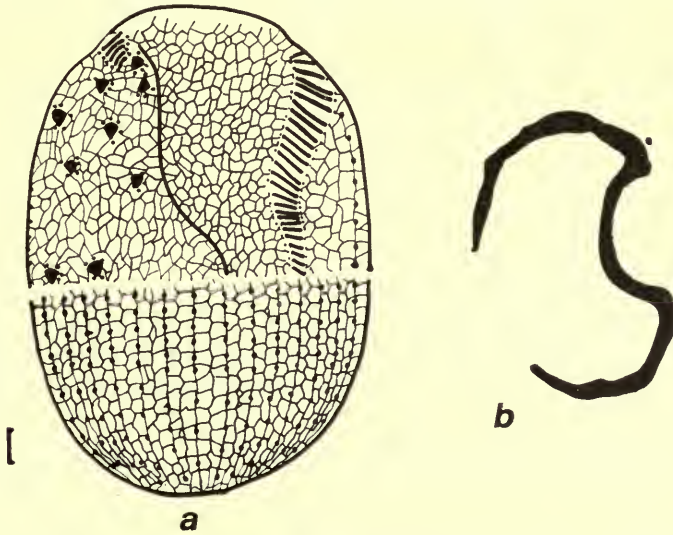


FIG. 14. *Euplotes amietii*. a. Ventral and dorsal argyromes. b. Nuclei.
(After Dragesco, 1970.)

Euplotes antarcticus Fenchel and Lee, 1972

The description of this species depends solely upon the brief original report by Fenchel and Lee (1972) based on material collected in Antarctica.

DIAGNOSIS. *Euplotes antarcticus* (Fig. 15) is a medium-sized (85 μm long, 30 μm wide) marine species. The shape is unlike that of other species in being very elongate and almost rectangular in outline except for the pointed posterior region. The peristome is long and narrow and there is a cleft in the right peristomial margin. The AZM is composed of approximately 30 membranelles and extends down $\frac{2}{3}$ of the body to the cytostome. The dorsal surface is clearly sculptured with 6 longitudinal ridges. The dorsal argyrome was not drawn very clearly but appears to be of the double-eurystomus type with 8 kineties carrying about 13 cilia in the mid-dorsal rows. There are 10 frontoventral, 5 transverse and 4 or 5 caudal cirri. The macronucleus is an elongate 3-shape.

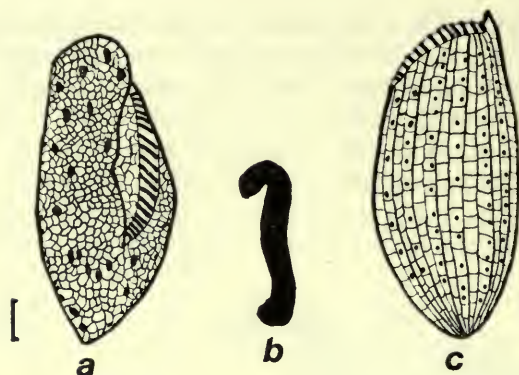


FIG. 15. *Euplotes antarcticus*. a. Ventral argyrome. b. Macronucleus. c. Dorsal argyrome. (After Fenchel & Lee, 1972.)

***Euplotes balteatus* (Dujardin, 1841) Kahl, 1932**

This species was first described by Dujardin (1841) and although the descriptions given were brief and incomplete they were just sufficient to enable Kahl (1932) to identify the species and present better diagrams. The morphology of the silver-line systems were not available until Tuffrau (1964) published his work on polymorphism in the species. In the present author's opinion the *E. balteatus* described by Burkovsky (1970) is *E. charon*.

DIAGNOSIS. *Euplotes balteatus* (Fig. 16) is highly variable (30–150 μm long) in size and the actual size depends to a great extent upon its food source (Tuffrau, 1964). This species has been found living in marine waters but has also been frequently recorded in the intestinal tract of certain sea urchins (*Allocentrus fragilis*,

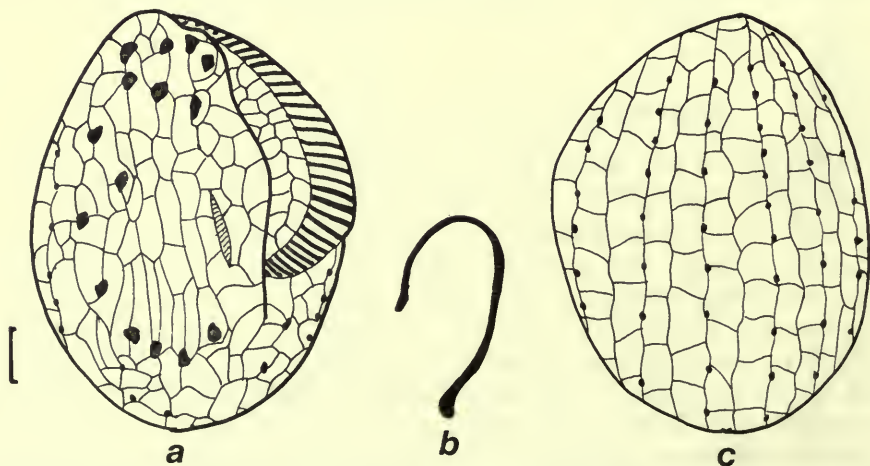


FIG. 16. *Euplotes balteatus*. a. Ventral argyrome. b. Macronucleus. c. Dorsal argyrome. (After Tuffrau, 1964.)

Strongylocentrotus droebachiensis, *S. ehinoides*, *S. franciscanus* and *S. purpuratus* – see Berger, 1965). The polymorphism of this organism is correlated with the AZM size which enlarges considerably when feeding upon ciliates such as *Philaster* sp. When feeding on bacteria there are 25–30 small membranelles but when feeding on other ciliates the membranelles are larger in size and there are then 70–80 in number. The dorsal argyrome is of the double-eurystomus type but is less regular than is usually found. Tuffrau (1964) reported that there are 8 dorsolateral kineties with up to 11 cilia in the mid-dorsal rows. There are 10 frontoventral, 5 transverse and 4 or 5 caudal cirri. The macronucleus is an open C-shape when feeding upon bacteria but more horse-shoe shaped when feeding on ciliates.

Euplotes bisulcatus Kahl, 1932

This species has been reported from marine sponges by Wenzel (1961) since its first description by Kahl (1932). Since that time Borror (1963) isolated it from algal growths in tidal marsh ponds and described its silver-line system.

DIAGNOSIS. *Euplotes bisulcatus* (Fig. 17) is a small (40 μ m long, 30 μ m wide) oval marine hypotrich. The dorsal surface has prominent double-edged ridges separated by shallow grooves parallel to the dorsal ciliary rows 4, 5 and 6. The ventral surface is also ridged and the central ridge is very conspicuous. The AZM extends almost $\frac{2}{3}$ down the length of the cell and is composed of about 17 membranelles. The dorsal argyrome is of the double-eurystomus type with 8 dorsolateral kineties bearing 5–7 cilia in the mid-dorsal rows. There are 9 frontoventrals, 5 transverse and 3 caudal cirri. The macronucleus is C-shaped with an adjacent anterior micronucleus.

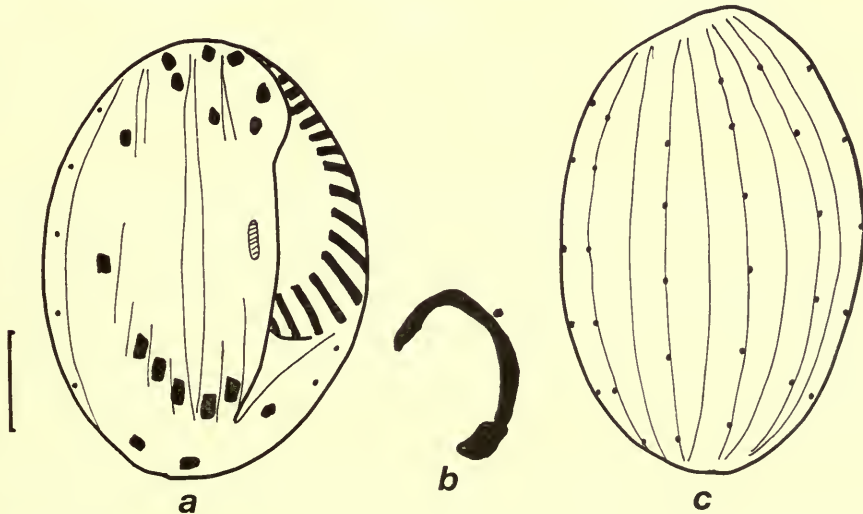


FIG. 17. *Euplotes bisulcatus*. a. Ventral aspect. b. Nuclei. c. Dorsal aspect.
(After Borror, 1963.)

Euplotes charon (Müller, 1786) Ehrenberg, 1830

This species has a long history and was described successively by Müller (1786), Ehrenberg (1830, 1833, 1838), Dujardin (1841) and Stein (1859). These descriptions vary considerably and it was not until almost a century later that Kahl (1932) gave a good succinct description of this species. Later Tuffrau (1960) and Borror (1963) were to describe the silver-line system. Tuffrau (1960) was of the opinion that *E. affinis* and *E. moebiusi* were synonyms of *E. charon* but recently Curds (1974) has demonstrated that these former two organisms are species in their own right.

DIAGNOSIS. *Euplotes charon* (Fig. 18) is a medium (70–96 μm long) oval marine species which has a very large open triangular peristomial region. The right margin

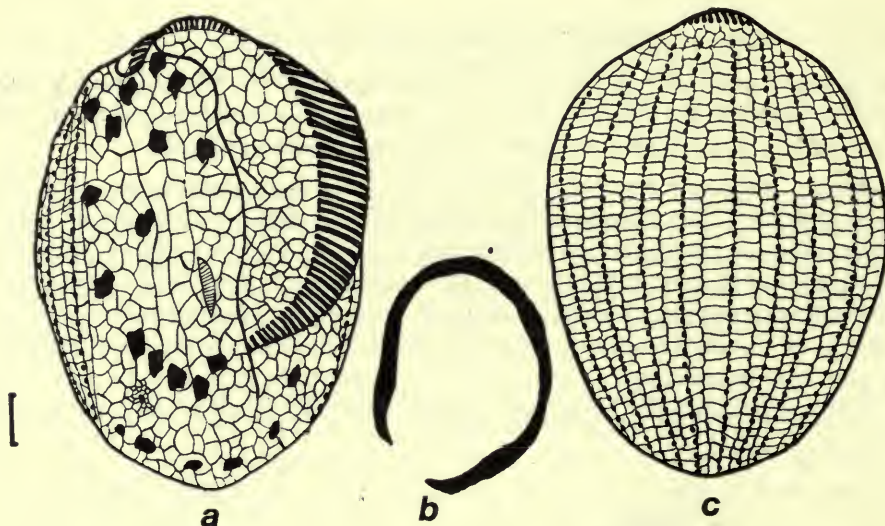


FIG. 18. *Euplotes charon*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

of the peristome winds sinusoidally down past the cytostome to about $\frac{2}{3}$ of the body length. The AZM bears approximately 70 strong membranelles while the AZM as a whole extends down to about $\frac{2}{3}$ of the body length. The dorsal argyrome is of the double-eurystomus type with 12 dorsolateral kineties carrying 35–40 dorsal cilia in the mid-dorsal rows according to Tuffrau (1960) but only 18–21 according to Borror (1963). There are 10 frontoventrals, 5 transverse and 5–8 caudal cirri. The macronucleus is horseshoe shaped and there is a small compact micronucleus situated anteriorly.

Euplotes crenosus Tuffrau, 1960

This species was first discovered and described by Tuffrau (1960) and has remained unmentioned since that time.

DIAGNOSIS. *Euplotes crenosus* (Fig. 19) is a small (50–70 μm long) freshwater oval hypotrich. There is a prominent notch at the anterior end of the cell which is coincident with a longitudinal depression on the ventral surface of the cell. The peristome is quite small and extends just over halfway down the body length. There are 25–30 membranelles in the adoral zone. The dorsal argyrome is of the double-eurystomus type with 8 dorsolateral kineties bearing up to about 23 cilia in the mid-dorsal rows. There are 10 frontoventral, 5 transverse and 4 caudal cirri. The macronucleus is C-shaped with the micronucleus situated half-way down the left border of the macronucleus.

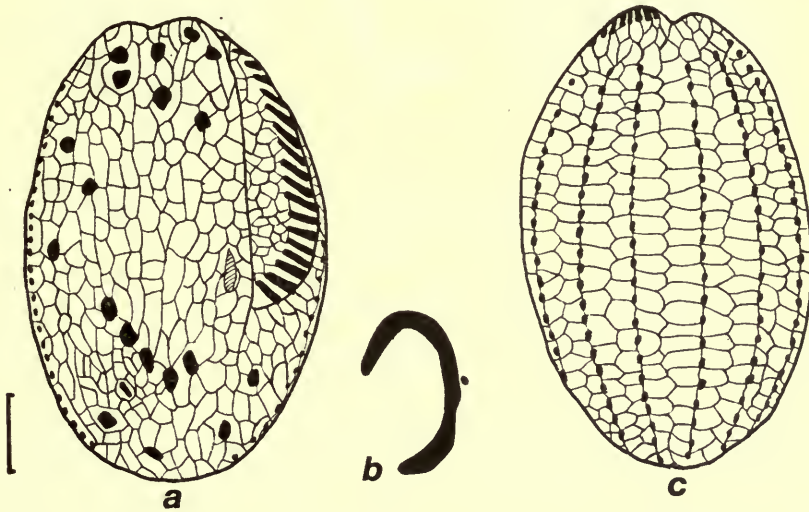


FIG. 19. *Euplotes crenosus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

Euplotes dogieli Agamaliev, 1967

This species has only been described once and that was from material found in sand samples taken from the Caspian Sea.

DIAGNOSIS. *Euplotes dogieli* (Fig. 20) is a small (60 μm long) marine species whose shape closely resembles that of *E. poljanskyi* Agamaliev, 1966 which is ellipsoid. The peristome is of medium size and it stretches about $\frac{2}{3}$ of the length of the cell. There is a definite curved indentation almost midway down the left peristomial margin. The AZM is composed of 35–38 membranelles and is rather narrow. The dorsal argyrome is of the double-eurystomus type with 7 dorsolateral kineties carrying about 13 cilia in the mid-dorsal rows. There are 9 frontoventral, 5 transverse and 3 caudal cirri. The macronucleus is C-shaped with the anterior curve being angular and acute. The compact micronucleus is situated to the left of this anterior angular bend.

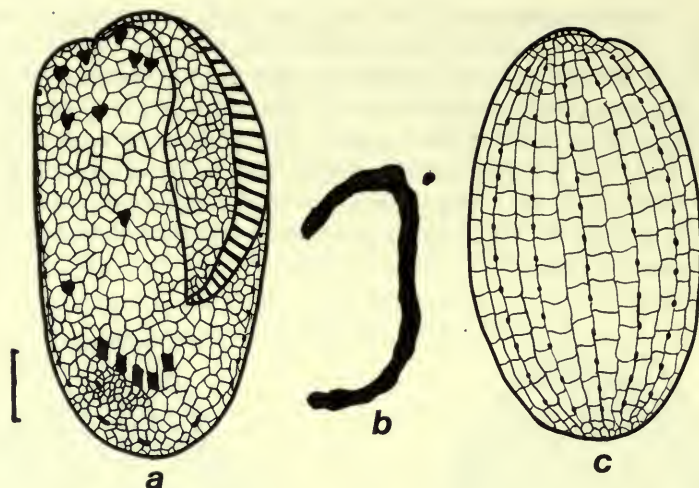


FIG. 20. *Euplotes dogieli*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome.
(After Agamaliev, 1967.)

Euplotes eury stomus (Wrzesniowski, 1870) Kahl, 1932

Difficulties over the identification of *E. eury stomus* and confusion of it with several other species is well documented but unfortunately is still perpetuated. Wrzesniowski (1870) originally described an organism which he named *E. patella* var. *eury stomus* Wrzesniowski, 1870 which was later elevated to the species level *E. eury stomus* (Wrzesniowski, 1870) Kahl, 1932. Pierson (1943) made a comparative study of several strains of *Euplotes* and four distinct species were described by him. One of these was *E. eury stomus* and one was a hitherto undescribed organism that was named *E. aediculatus* Pierson, 1943. It was not until Tuffrau (1960) introduced silver impregnation methods to *Euplotes* taxonomy that *E. patella* could readily be distinguished from *E. eury stomus* and *E. aediculatus*; unfortunately Tuffrau (1960) also introduced a considerable amount of confusion since he described *E. aediculatus* but called it *E. eury stomus* and described *E. eury stomus* but called it *E. plumipes* Stokes, 1884. Even though Pierson, Gierke and Fisher (1968) pointed out the errors of Tuffrau (1960), Carter (1972) disregarded the evidence and followed the scheme of Tuffrau (1960). Thus Carter (1972) also described *E. aediculatus* under the name of *E. eury stomus* and *E. eury stomus* under the name *E. plumipes*; furthermore, this latter author reintroduced the species *E. variabilis* Stokes, 1887 which in the opinion of the present author is a variant of *E. eury stomus*.

It is evident from the original diagrams given by Wrzesniowski (1870) (see Fig. 21b) that the shape of the AZM is definitely sigmoidal and Kahl (1932) placed particular emphasis upon this shape as being a distinctive and immediately visible feature. A comparison of the original diagrams in Figs. 21a and 21b of *E. plumipes* drawn by Stokes (1884) and *E. patella* var. *eury stomus* drawn by Wrzesniowski (1870) shows that both have a sigmoidal AZM and in fact have long been regarded as synonymous

species (Kahl, 1932; Borror, 1972). The sigmoidal shape of the AZM is also obvious in the silver preparations of *E. plumipes* and *E. variabilis* (Fig. 22) drawn by Carter (1972). In the descriptions that follow *E. eurystomus* (Figs. 23, 24) is regarded as was originally intended by Wrzesniowski (1870) and Kahl (1932), not as by Tuffrau (1960) and Carter (1972).

DIAGNOSIS. *Euplotes eurystomus* (Figs. 22, 23, 24) is a large (100–160 μm long, 40–90 μm wide) ovoid freshwater hypotrich. The buccal overture is triangular

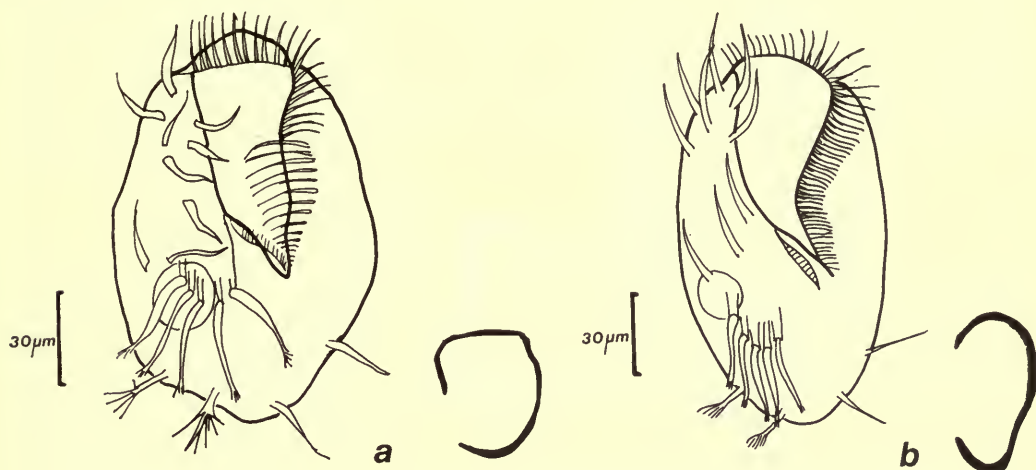


FIG. 21. Species synonymous with *Euplotes eurystomus*. a. Ventral aspect and macro-nucleus of *Euplotes plumipes*. (After Stokes, 1884.) b. Ventral aspect and macro-nucleus of *Euplotes patella* var. *eurystomus*. (After Wrzesniowski, 1870.)

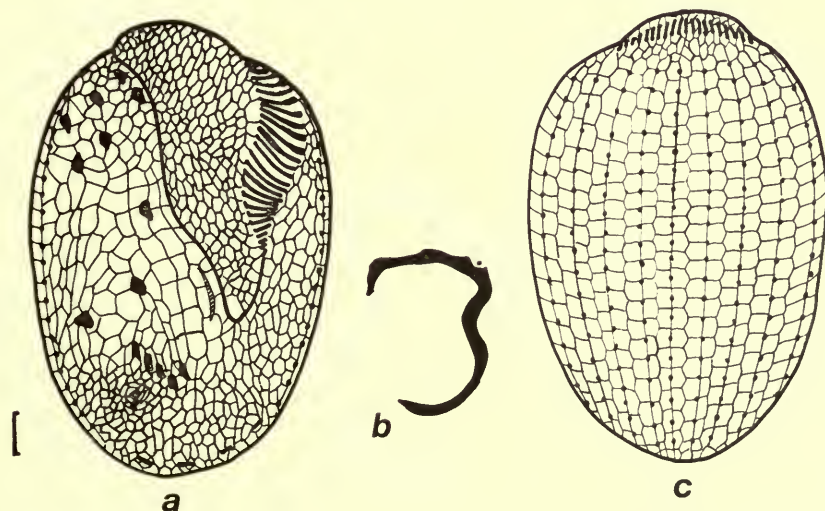


FIG. 22. *Euplotes variabilis*, a species synonymous with *Euplotes eurystomus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Carter, 1972.)

and there is a single anterior peristomial pouch. The AZM collar is high and prominent. The AZM is markedly sigmoid in shape and contains 50–65 membranellae. There are 9 frontoventral, 5 transverse and commonly 4 caudal cirri although Carter (1972) found 5 caudals in one specimen. The arrangement of cirri is shown in Figs. 22, 23 and 24. The dorsal argyrome is typical of the double-eurystomus type with 10 dorsolateral kineties although Carter (1972) reported two strains that had a

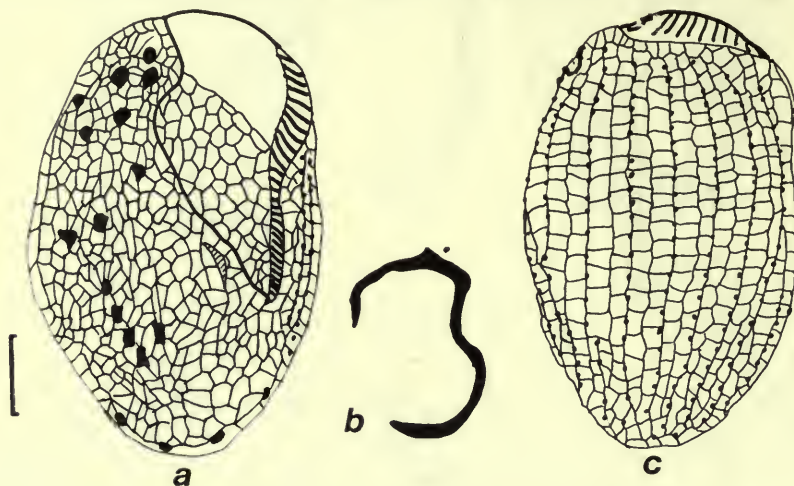


FIG. 23. *Euplotes eurystomus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Pierson, Gierke & Fisher, 1968.)

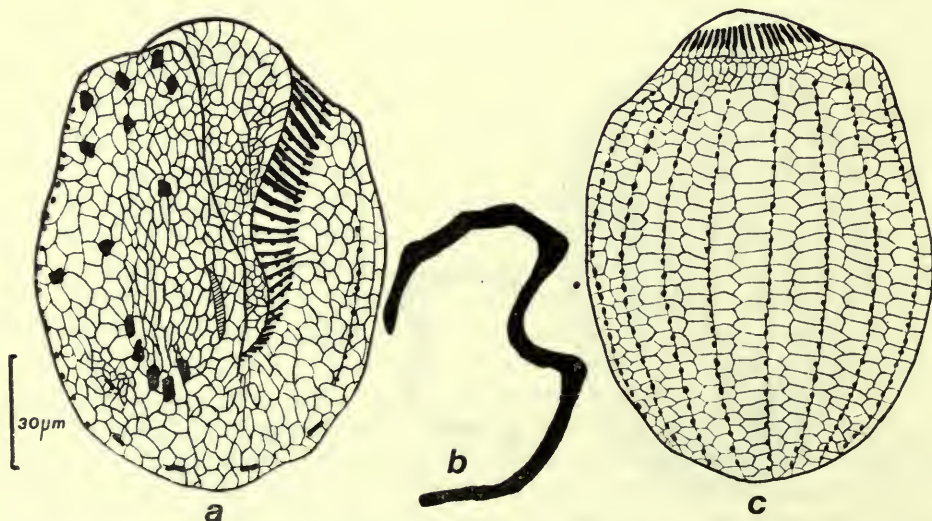


FIG. 24. *Euplotes eurystomus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (Called *Euplotes aediculatus* in Tuffrau, 1960.)

variable number (8–12) of kineties. The dorsal and ventral silver-line systems are shown in Figs. 22, 23 and 24. There are 17–25 dorsal cilia in the central kineties.

The macronucleus is typically 3-shaped and there is sometimes a definite concave notch which contains the micronucleus. Carter (1972) believed that the nuclear pattern, the sigmoidal AZM, the possession of an anterior peristomial pouch and a wide variation in the numbers of dorsolateral kineties were sufficient to distinguish two strains of *Euplotes* from *E. eurystomus* and proposed the restoration of the species *E. variabilis* Stokes, 1884. However, a similar nuclear pattern was observed by Pierson (1943) in *E. eurystomus*; the sigmoidal AZM has already been stated to be a characteristic feature of *E. eurystomus* which species also has an anterior peristomial pouch. In the present author's opinion the variability of the numbers of dorsolateral kineties is not in itself sufficient to distinguish *E. variabilis* Stokes from *E. eurystomus*.

Euplotes harpa Stein, 1859

This species was first properly described by Stein (1859) although Dujardin (1841) seems to have been the first to see this organism which he called *Ploesconia cithara*. Wallengren (1900, 1901) gave the first good diagram of *E. harpa* and these conform well with the descriptions of Stein (1859). Although Chatton made silver preparations of this species in 1939 these were not published until Tuffrau (1960) did so with new specimens collected in 1955.

DIAGNOSIS. *Euplotes harpa* (Fig. 25) is a large (150–160 μm long) marine species with a more or less oval shape, although the left side is always more curved than the other. The peristome is large and open and there is a conspicuous lip on the right margin. The AZM is very curved and extends about $\frac{2}{3}$ down the length of the body. There are approximately 65–70 membranelles in the AZM. The dorsal argyrome is of the double-eurystomus type with 13 dorsolateral kineties bearing 40–45 dorsal cilia in the central rows. There are 10 frontoventral, 5 transverse and 4 caudal cirri. The macronucleus is an open C-shape with tendencies towards a 3-shape. The micronucleus is in an anterior position.

Euplotes inkystans Chatton in Tuffrau, 1960

Although this species was discovered by Chatton in the 1950's it was not described by him but preparations that he made were described by Tuffrau (1960).

DIAGNOSIS. *Euplotes inkystans* (Fig. 26) is a medium (70–80 μm long) freshwater oval species. There is a prominent notch on the right of the peristomial collar which is narrow but rounded. The peristome is long and extends almost $\frac{3}{4}$ down the length of the cell. The AZM is composed of approximately 40 membranelles. The dorsal argyrome is of the double-eurystomus type and there are 10 dorsolateral kineties with about 25 dorsal cilia in the central rows. There are 10 frontoventral, 5 transverse and 4 (or rarely 5) caudal cirri. The macronucleus is a simple open C-shape with the micronucleus lying on the left border.

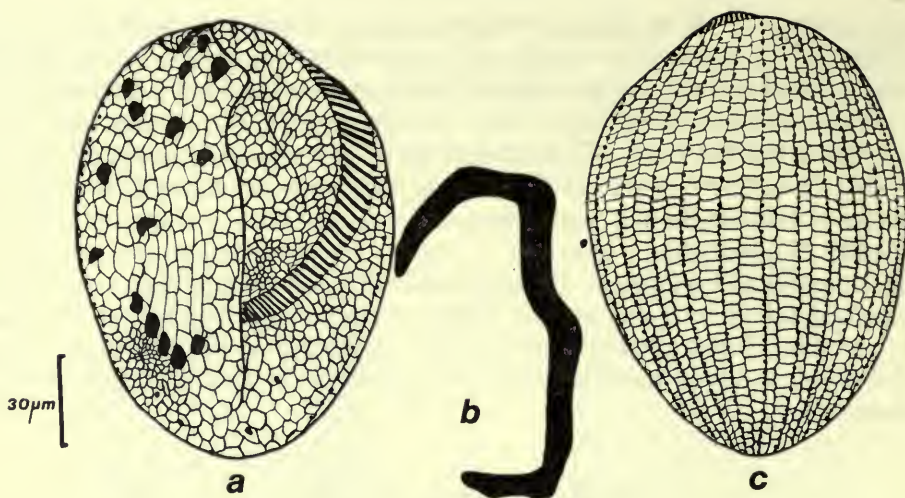


FIG. 25. *Euplotes harpa*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

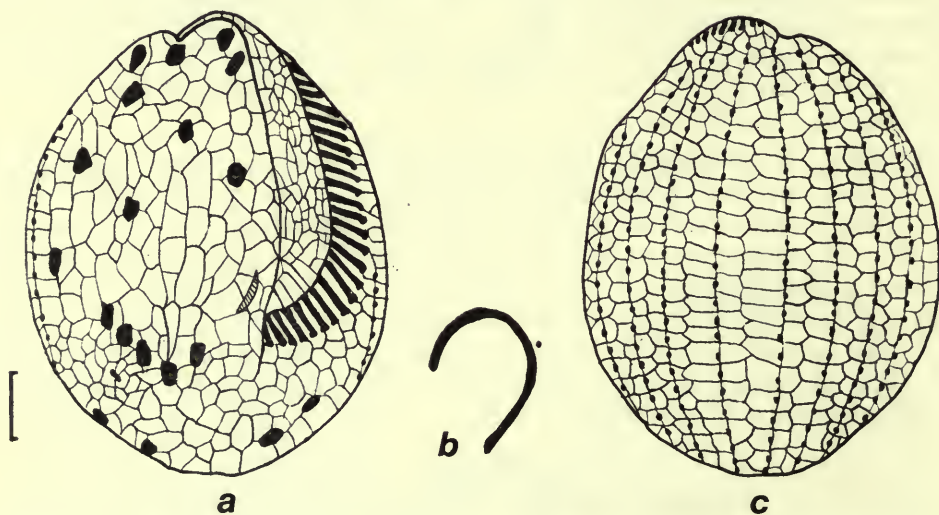


FIG. 26. *Euplotes inkystans*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

Euplotes latus (Agamaliev, 1967)

Euplotes latus was described by Agamaliev (1967) under the name *E. patella* forma *latus* Kahl, 1932. However, it is evident from the silver-line system that this species cannot be a form of *E. patella* for several reasons (compare Figs. 27 and 40); for example *E. latus* has a double-eurystomus type of dorsal argyrome whereas *E. patella* has a double-patella type, the numbers of kineties and dorsal cilia are different and

the shapes of the macronuclei are different. However, it is also clear that the organism described by Agamaliev (1967) does not conform to any others described to date and the present author considers it sufficiently different to warrant elevating it to a species in its own right.

DIAGNOSIS. *Euplotes latus* (Fig. 27) is a medium (70 μm long) marine species that is broadly rounded posteriorly but narrows anteriorly. The peristome is large and extends just over $\frac{2}{3}$ down the length of the cell. The AZM is broadly curved and is composed of 35–40 membranelles. The dorsal argyrome is of the double-eurystomus type with only 6 dorsolateral kineties bearing up to 15 dorsal cilia in the central rows. There are 9 frontoventral, 5 transverse and 4 caudal cirri. The two centrally positioned frontoventral cirri (V_2 and VI_2) are situated very close together. The macronucleus is an open angular C-shape with a micronucleus situated close to the left anterior border.

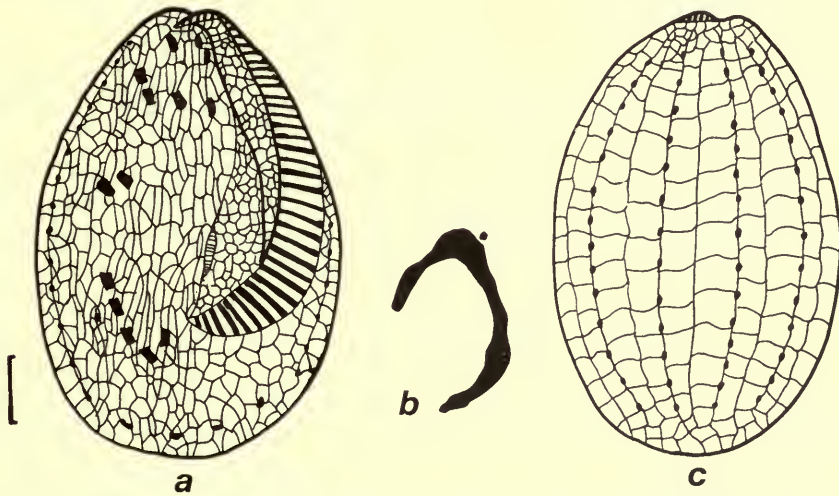


FIG. 27. *Euplotes latus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (Called *Euplotes patella* forma *latus* in Agamaliev, 1967.)

Euplotes magnicirratus Carter, 1972

This species is one of the four new species described recently by Carter (1972).

DIAGNOSIS. *Euplotes magnicirratus* (Fig. 28) is a small (54 μm long, 40 μm wide) oval marine species. The peristomial cavity is rather wide and extends approximately $\frac{3}{4}$ of the length of the cell. The AZM is composed of about 50 membranelles and is relatively straight for the majority of its length and then sharply curves in towards the cytostome. The dorsal surface is convex and prominently ridged. The dorsal argyrome is of the double-eurystomus type but the polygons are rather more square than is usual. There are 8 dorsolateral kineties each containing 13–17 dorsal cilia except the left lateral one which is short and contains only 5–8 cilia. The transverse cirri are particularly large and there are 10 frontoventrals, 5 transverse and 4 caudal

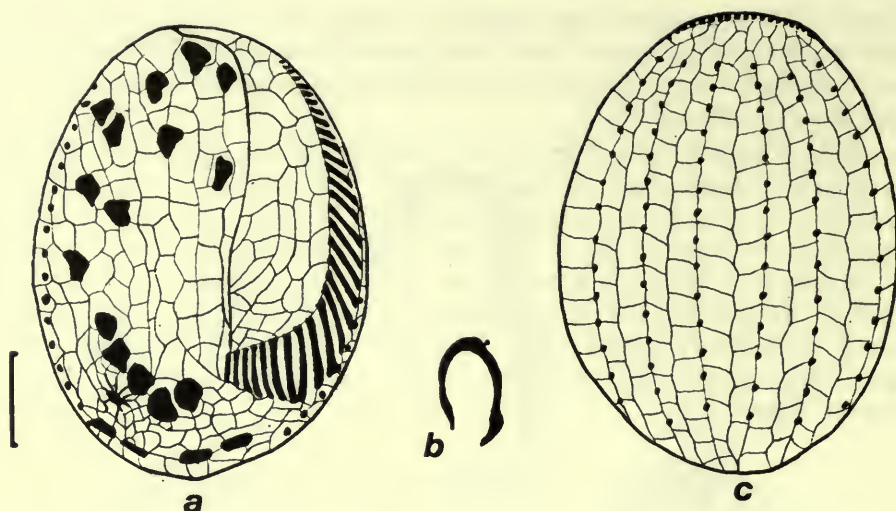


FIG. 28. *Euplotes magnicirratu*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Carter, 1972.)

cirri. The macronucleus is an irregular hoop-shape and is highly characteristic of the species, since both ends are pointed. The micronucleus is situated in a small depression in the upper left border of the macronucleus.

Euplotes neapolitanus Wichterman, 1964

This species was first described briefly by Wichterman (1962a, b) and later (1964) more precisely from material collected from 50–60 metres in the proximity of the Bay of Naples.

DIAGNOSIS. *Euplotes neapolitanus* (Fig. 29) is a large (130 μm long, 70 μm wide) marine species that is ellipsoidal in shape although the anterior is often wider and more truncated than the posterior. The peristome is conspicuous and extends approximately $\frac{2}{3}$ down the body length. The AZM is composed of about 65 membranelles. The dorsal argyrome is of the double-eurystomus type consisting of 11 dorsolateral kineties with about 18 cilia in the mid-dorsal rows. There are 10 fronto-ventral, 5 transverse and 4 caudal cirri. The macronucleus is C-shaped but both arms point posteriorly and the small spherical micronucleus lies in the middle of the body on the left of the macronucleus.

Euplotes octocirratu Agamaliyev, 1967

Agamaliyev (1967) described this species from samples of sand collected from the Caspian Sea.

DIAGNOSIS. *Euplotes octocirratu* (Fig. 30) is a small (55–60 μm long) marine hypotrich that is more or less oval in outline although the posterior is rather narrower

than the anterior. The peristome is quite large and extends $\frac{2}{3}$ down the length of the cell. The AZM is regularly curved and is composed of about 30 membranelles. The dorsal argyrome is of the double-eurystomus type with 7 dorsolateral kineties carrying up to 14 cilia in the mid-dorsal rows. There are 10 frontoventral, 5 transverse and 3 caudal cirri. The macronucleus is an angular C-shape with a compact micronucleus in an anterior position.

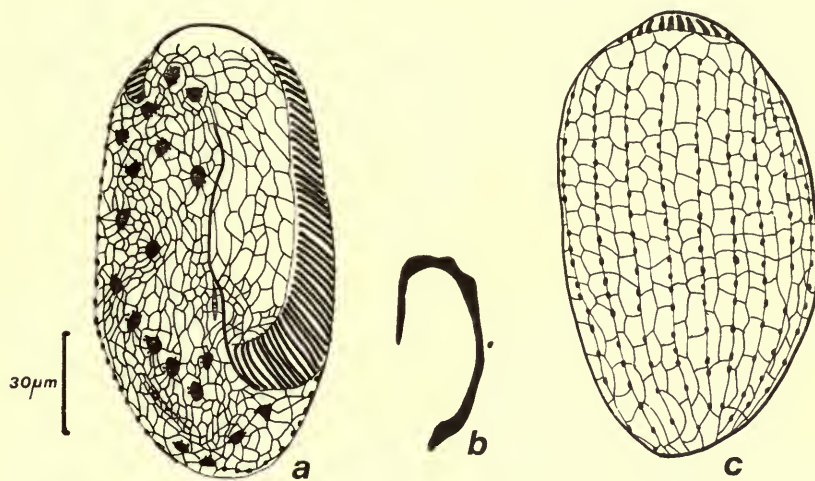


FIG. 29. *Euplotes neapolitanus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Wichterman, 1964.)

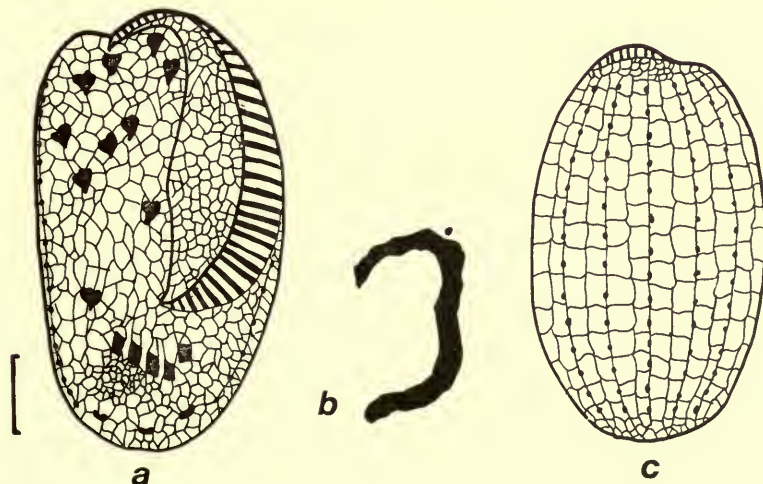


FIG. 30. *Euplotes octocirratus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Agamaliev, 1967.)

Euplotes parkei Curds, 1974

This species is a recent addition to the genus.

DIAGNOSIS. *Euplotes parkei* (Fig. 31) is a small (40 μm long, 30 μm wide) euryhaline species that is broadly oval in outline. The dorsal surface has 6 inconspicuous low longitudinal ridges and the ventral surface has 7 minor ridges. The AZM is about $\frac{2}{3}$ of the body length and composed of 18 membranelles. A deep pocket near the cytostome contains an undulating membrane. There are usually 8 but occasionally 9 frontoventral, 5 transverse and 4 caudal cirri. The dorsal argyrome is of the double-eurystomus type with 8 dorsolateral kineties bearing a maximum of 11 cilia in the mid-dorsal rows. The ventral argyrome consists of a series of few but large polygons and resembles that of *E. cristatus* (see Tuffrau, 1960). The macronucleus is C-shaped and the micronucleus is situated close to its left anterior edge.

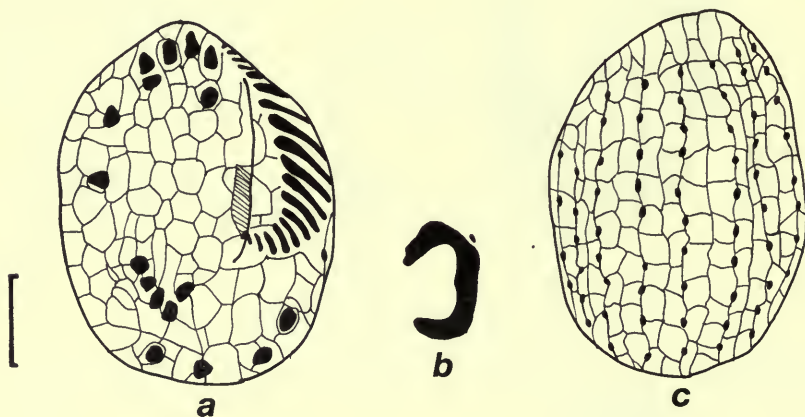


FIG. 31. *Euplotes parkei*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Curds, 1974.)

Euplotes poljanskyi Agamaliyev, 1966

This species has been described on two occasions by Agamaliyev (1966, 1967) from samples of sand collected from the Caspian Sea.

DIAGNOSIS. *Euplotes poljanskyi* (Fig. 32) is a small to medium-sized (55–70 μm long) marine ciliate. It has an elongated ellipsoidal shape with a medium-sized peristome that is strongly concave on the right margin. The narrow AZM is composed of 36–40 membranelles, and it extends down to about $\frac{2}{3}$ the body length. The dorsal argyrome is of the double-eurystomus type with 7 dorsolateral kineties bearing 10–12 dorsal cilia in the central rows. There are 8 frontoventral, 5 transverse and 3 caudal cirri. The macronucleus is C-shaped and both ends are bluntly narrower than the central regions. The micronucleus lies in an anterior position.

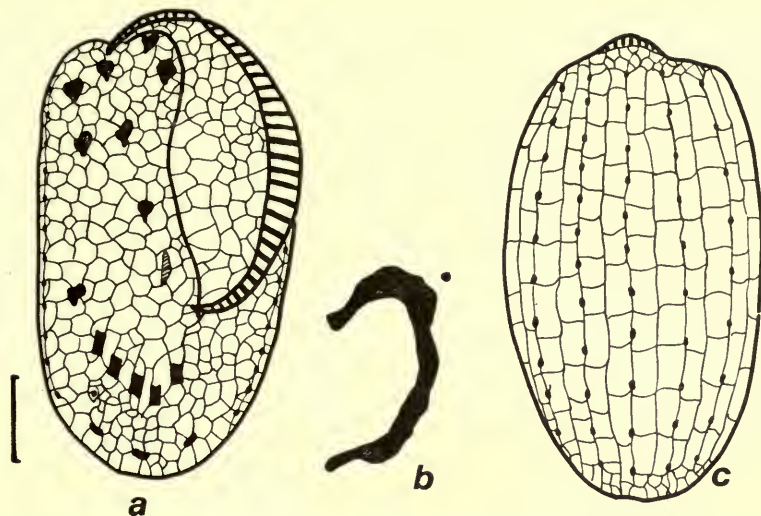


FIG. 32. *Euplotes poljanskyi*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Agamaliev, 1966.)

Euplotes polycarinatus Carter, 1972

Recognition of this species relies upon the recent description of Carter (1972).

DIAGNOSIS. *Euplotes polycarinatus* (Fig. 33) is a medium (90 μm long, 80 μm wide) almost triangular shaped marine hypotrich. The shape of the AZM is one of its most distinctive features as it is very wide and crescent-like with 60–76 membranelles. The dorsal surface is slightly ridged and the dorsal argyrome is of the double-eurystomus type with 20 narrowly spaced dorsolateral kineties bearing up to 23 dorsal cilia. A few specimens have been seen with 21 dorsolateral kineties. The ventral surface is flat and there are 10 frontoventral, 5 transverse and 5–9 caudal cirri. The macronucleus is a highly irregular 3-shape with a deep involution on the upper right border within which the compact micronucleus lies.

Euplotes quinquecarinatus Gelei, 1950

The general morphology of this species was first briefly described by Gelei (1950) and the silver-line system was added later by Borror (1968a).

DIAGNOSIS. *Euplotes quinquecarinatus* (Fig. 34) is a small (55 μm long, 40 μm wide) marine species whose general outline shape tends to be oval although there may be conspicuous wing-like extensions to the ridges associated with dorsal cilium rows 1, 3 and 7. The AZM is small and extends halfway down the body length and contains 25–30 membranelles. The dorsal argyrome is of the double-eurystomus type with 9 dorsolateral kineties carrying 13–15 cilia in the mid-dorsal rows. There are 9 frontoventral, 5 transverse and 4 caudal cirri. The macronucleus is C-shaped and the micronucleus lies in an anterior position.

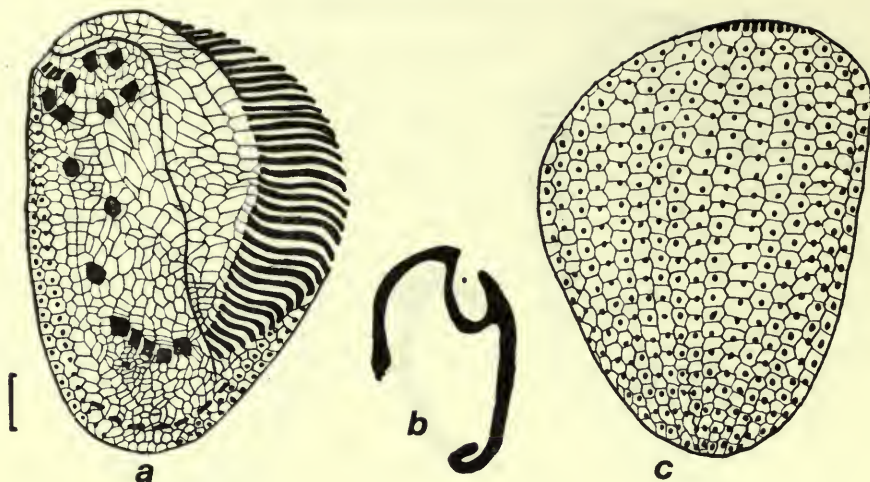


FIG. 33. *Euplotes polycarinatus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Carter, 1972.)

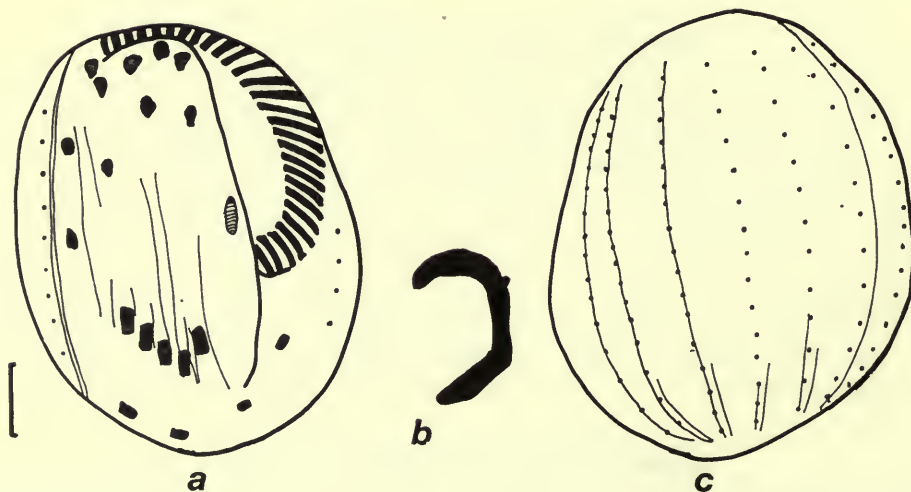


FIG. 34. *Euplotes quinquecarinatus*. a. Ventral aspect. b. Nuclei. c. Dorsal aspect. (After Borror, 1968a.)

Euplotes trisulcatus Kahl, 1932

Kahl (1932) originally found this species in marine aquariums and gave sufficiently precise diagrams and descriptions to enable Tuffrau (1960), Borror (1963) and Carter (1972) to identify this species in other marine samples. The descriptions of the silver-line system of this species given both by Tuffrau (1960) and Carter (1972) are identical.

DIAGNOSIS. *Euplotes trisulcatus* (Fig. 35) is a small ($40\ \mu\text{m}$ long, $30\ \mu\text{m}$ wide) form that has been only recorded in marine habitats. The shape of the body is distinctive in that it is prominently narrower at its posterior end. There is a pronounced extension of the right side of the body beyond the peristomial collar. The peristomial cavity is long and narrow extending about $\frac{2}{3}$ down the body. The AZM is evenly curved along the outer border of the peristome and contains 25–36 membranelles. The dorsal surface is deeply ridged showing three prominent furrows. The dorsal argyrome is of the double-eurystomus type and there are 7 dorsolateral kineties with a maximum of 11 dorsal cilia widely separated in the central rows. There are 10 frontoventral, 5 transverse and 4 caudal cirri although Borror (1963) reported the presence of only 3 caudals. The macronucleus is a very open C-shape with angular rather than rounded ends. The micronucleus is compact and is situated anteriorly near the upper left border of the macronucleus.

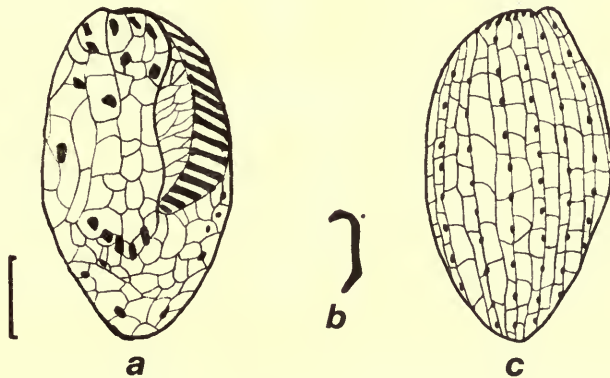


FIG. 35. *Euplotes trisulcatus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

Euplotes tuffraui Berger, 1965

Euplotes tuffraui was described by Berger (1965) from samples taken from the posterior digestive tract of three species of sea urchins.

DIAGNOSIS. *Euplotes tuffraui* (Fig. 36) is a large ($113\ \mu\text{m}$ long, $73\ \mu\text{m}$ wide) marine species that is found in the digestive tract of stronglylocentrotid echinoids. The three urchins that have to date been reported to contain this species are *Allo-centrotus fragilis*, *Strongylocentrotus echinoides* and *S. purpuratus*. The shape of the body is narrowly pyriform with the anterior end often being distinctly pointed. The AZM is just over half the length of the body and is composed of 40–45 membranelles. The dorsal surface is sculptured longitudinally with 7 ridges. The dorsal argyrome is of the double-eurystomus type but irregular with 10 (rarely 9) dorso-lateral kineties with 8–11 dorsal cilia per kinety. There are 8–10 frontoventral cirri depending upon the degree of fusion of the infraciliary bases in rows III and IV. There are 5 transverse and 4 caudal cirri. The macronucleus is C-shaped with a compact anterior micronucleus.

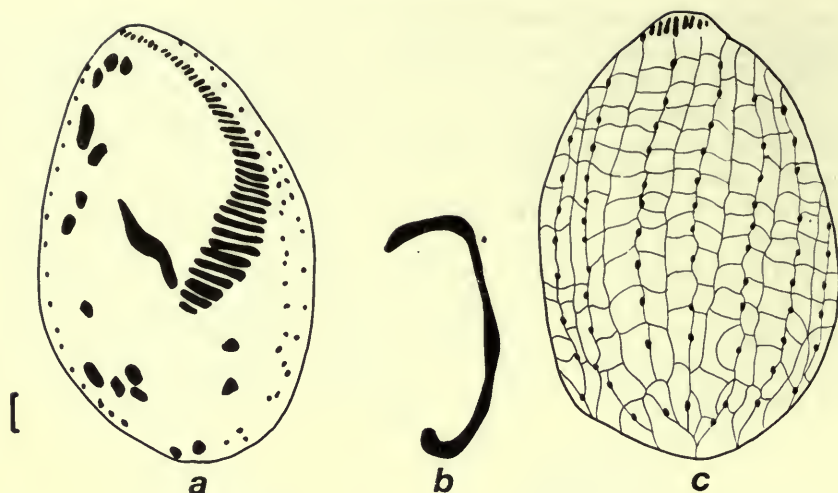


FIG. 36. *Euplotes tuffraui*. a. Ventral aspect. b. Nuclei. c. Dorsal argyrome. (After Berger, 1965.)

SECTION C. KEY TO SPECIES WITH A DOUBLE-PATELLA TYPE DORSAL ARGYROME

- | | | |
|------|--|-------------------------|
| 36 a | Double dorsal argyrome with large polygons on right and small polygons on left of kineties | 37 |
| b | Double dorsal argyrome with large polygons on left and small polygons on right of kineties | 38 |
| 37 a | 9 frontoventral and 5 transverse cirri | <i>E. zenkewitchi</i> |
| b | 8 frontoventral and 6 transverse cirri | <i>E. strelkovi</i> |
| 38 a | 7 or less dorsolateral kineties, 7, 8 or 10 frontoventral cirri | 39 |
| b | 8 or more dorsolateral kineties, 9 frontoventral cirri | 40 |
| 39 a | 10 frontoventral cirri, 6 or less dorsal cilia in central kineties | <i>E. rariseta</i> |
| b | 7 or 8 frontoventral cirri, 11-15 dorsal cilia in central kineties | <i>E. raikovi</i> |
| 40 a | 8 dorsolateral kineties | <i>E. octocarinatus</i> |
| b | 9 dorsolateral kineties | 41 |
| 41 a | With symbiotic green algae and about 60 membranelles in AZM | <i>E. diadaleos</i> |
| b | Usually without symbionts, 30-35 membranelles in AZM | 42 |
| 42 a | 11-15 dorsal cilia in central kineties | <i>E. apsheronicus</i> |
| b | 25-30 dorsal cilia in central kineties | <i>E. patella</i> |

SECTION C. DESCRIPTIONS OF SPECIES

Euplotes apsheronicus Agamaliev, 1966

This organism was originally described by Agamaliev (1966) from specimens collected from sand samples from the Caspian Sea. A year later the same author redescribed the species (Agamaliev, 1967) with a few amendments to the original description.

DIAGNOSIS. *Euplotes apsheronicus* (Fig. 37) is a small (50-60 μm long) marine species that is ellipsoid in shape. There is a distinct peristomial collar and the

peristome is of medium size being just over half the body length. The AZM is composed of 30–35 membranelles. The dorsal argyrome is of the double-patella type with 9 dorsolateral kineties (not 7–8 as originally given by Agamaliev, 1966) and these bear about 15 cilia in the mid-dorsal rows. There are 9 frontoventral, 5 transverse and 4 caudal cirri. The macronucleus is an angular and very open C-shape with a micronucleus located anteriorly.

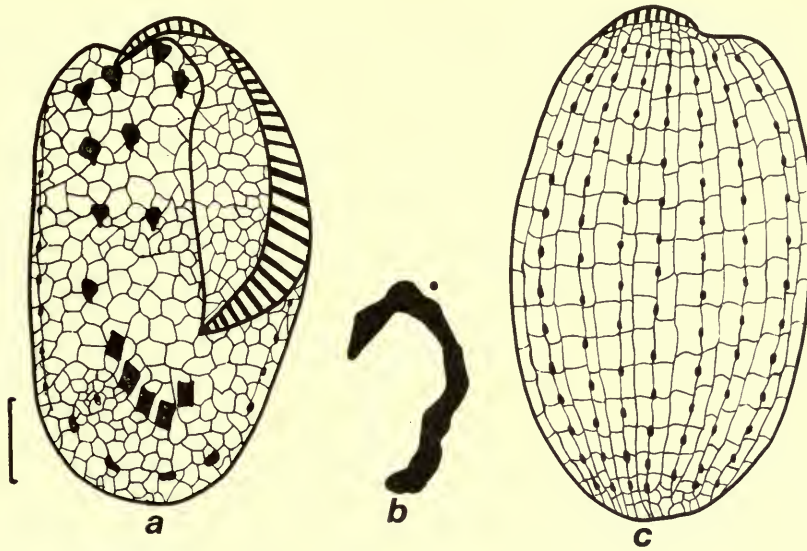


FIG. 37. *Euplotes apsheronicus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Agamaliev, 1966.)

Euplotes diadaleos Diller and Kounaris, 1966

This species has been recorded on one occasion only when Diller and Kounaris (1966) isolated it from an artificial pond in Pennsylvania, U.S.A.

DIAGNOSIS. *Euplotes diadaleos* (Fig. 38) is a medium (92 μm long, 57 μm wide) freshwater species that contains symbiotic zoochlorellae. The body is generally flattened and oval in outline. The peristome extends slightly beyond the midline of the body. The AZM consists of about 40–45 membranelles that curve smoothly to the cytostome. The dorsal argyrome is of the double-patella type with 9 dorso-lateral kineties containing 15–20 cilia in the mid-dorsal rows. There are 9 fronto-ventral, 5 transverse and 4 caudal cirri. The macronucleus is an angular C-shape with the anterior micronucleus in a shallow depression of the macronucleus.

Euplotes octocarinatus Carter, 1972

Euplotes octocarinatus is a recent addition to the genus and the only description available is that by Carter (1972).

DIAGNOSIS. *Euplotes octocarinatus* (Fig. 39) is a medium (80 μm long, 50 μm wide) freshwater ellipsoid species. The peristome is triangular in shape and it extends about halfway down the length of the body. The AZM is narrow as it emerges from the dorsal anterior collar and then widens towards the middle of the body, it contains about 36–42 membranelles. There is a well-defined pouch to the right of the peristomial cavity. The dorsal surface is convex and ridged. The dorsal

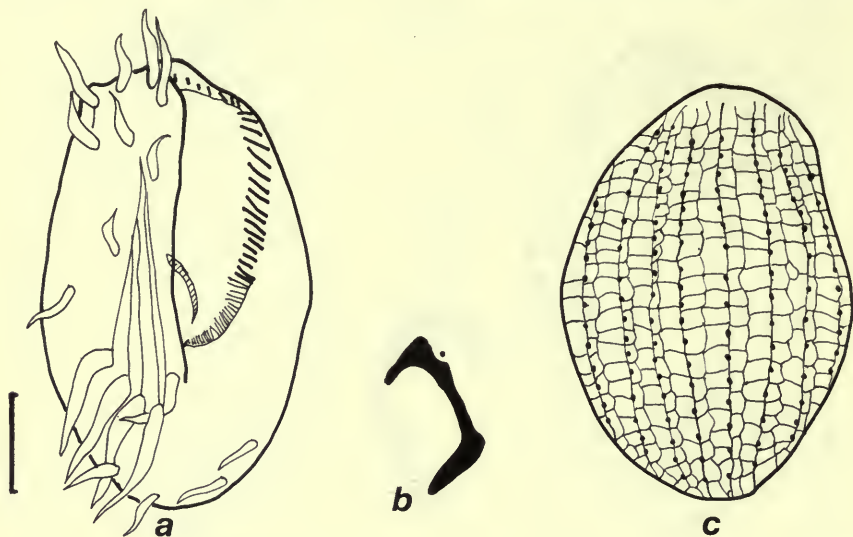


FIG. 38. *Euplotes diadaleos*. a. Ventral aspect. b. Nuclei. c. Dorsal argyrome. (After Diller & Kounaris, 1966.)

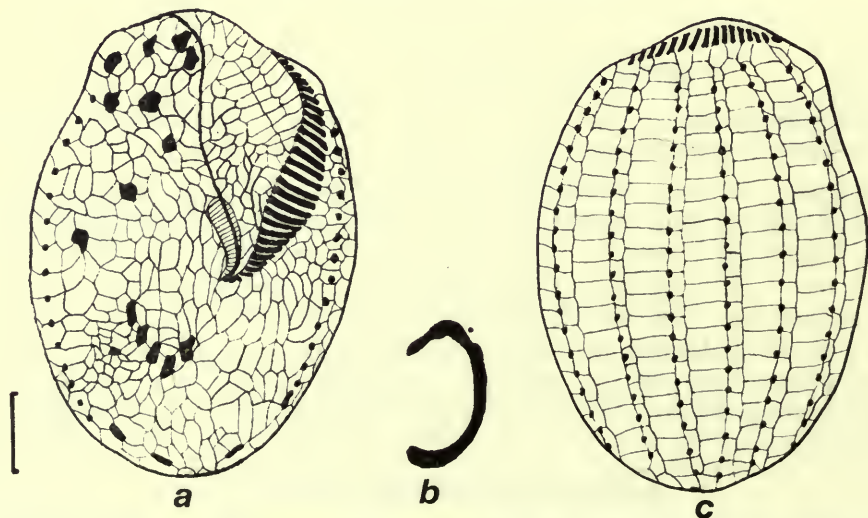


FIG. 39. *Euplotes octocarinatus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Carter, 1972.)

argyrome is of the double-patella type with 8 dorsolateral kineties containing 18–21 cilia in the mid-dorsal rows. There are 9 frontoventral, 5 transverse and 4 caudal cirri, although occasionally there may be 5 caudals. The macronucleus is a wide-mouthed C-shape and there is a small adjacent micronucleus.

Euplotes patella (Müller, 1773) Ehrenberg, 1838

Euplotes patella has a long historical record and has several synonyms; it was first described by Müller (1773) under the name *Trichoda patella* and subsequently by Müller (1786) as *Kerona patella*. It was called *E. patella* by Ehrenberg (1838) but was then named *Ploesconia patella* by Dujardin (1841). Several other early authors also refer to this species and much later Kahl (1932) found it necessary to subdivide the species into five forms which he named formae *typicus*, *latus*, *alatus*, *planctonicus* and *variabilis* (Stokes, 1887). These subdivisions were criticized by Pierson (1943) who observed that the first four of the above-mentioned forms were simply temporary varieties that could be found within clonal cultures of *E. patella*. Pierson (1943) also stated that *E. patella* forma *variabilis* Kahl, 1932 was in fact a variety of *E. eurystomus*. It was not until the work of Tuffrau (1960) that *E. patella* could readily be distinguished from *E. eurystomus* but with silver-line preparations this is now quite a simple task.

DIAGNOSIS. *Euplotes patella* (Fig. 40) is a large (110 μ m long, 65 μ m wide) oval freshwater species that has a pronounced blunt posterior end. The peristome is large, wide and almost triangular in appearance extending just over halfway down the length of the body. The AZM is narrow, evenly curved and contains 44–50 membranelles. The dorsal argyrome is of the double-patella type with 9 dorsolateral

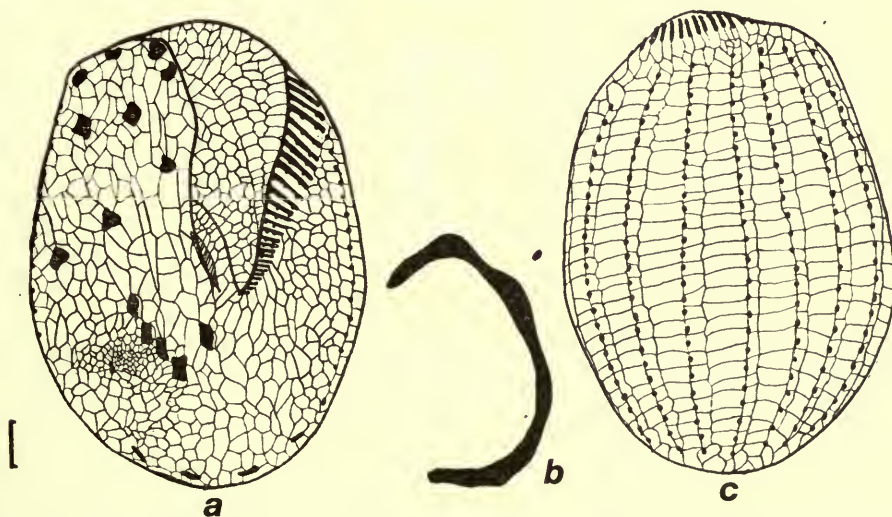


FIG. 40. *Euplotes patella*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

kineties containing about 26 cilia in the mid-dorsal rows, although it should be noted that Carter (1972) observed rather fewer cilia (13-19). There are 9 frontoventral, 5 strong transverse and 4 caudal cirri. The macronucleus is an open C-shape with slightly pointed extremities. The upper arm points down slightly and bears several indentations. The micronucleus is situated anteriorly.

Euplotes raikovi Agamaliyev, 1966

This species was first described by Agamaliyev (1966) and slightly amended later (Agamaliyev, 1967).

DIAGNOSIS. *Euplotes raikovi* (Fig. 41) is a small (50-60 μm long) marine ciliate whose outline body shape is broadly rounded. The peristome is of medium size and extends about $\frac{2}{3}$ down the body length. The AZM is regularly curved and contains 30-35 membranelles. The dorsal argyrome is of the double-patella type with 7 dorsolateral kineties bearing up to 11 cilia in the mid-dorsal rows. There are 7 or 8 frontoventral, 5 transverse and 3 caudal cirri. The macronucleus was originally reported to be a simple C-shape by Agamaliyev (1966) but less like a C in his later description (Agamaliyev, 1967) (see Fig. 41). The micronucleus is small and situated anteriorly.

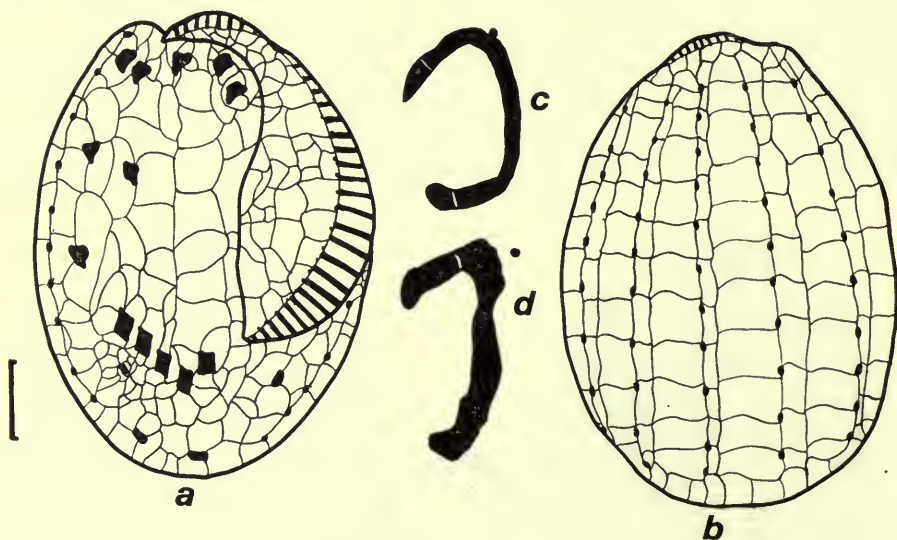


FIG. 41. *Euplotes raikovi*. a. Ventral argyrome. b. Dorsal argyrome. (After Agamaliyev, 1966.) c-d. Nuclei (after Agamaliyev, 1966 and 1967 respectively).

Euplotes rariseta Curds, West and Dorahy, 1974

This species was first described by Borror (1963) but he called it *E. moebiusi* Kahl, 1932. Curds, West and Dorahy (1974) isolated a marine hypotrich which in their opinion did not conform to any previous descriptions and named their organism *E.*

rariseta. Curds (1974) also described *E. moebiusi* Kahl, 1932 which agreed precisely with the descriptions of Kahl (1932) but differed in several respects from *E. rariseta*. There seems little doubt that *E. moebiusi* Borror, 1963 is the species described by Curds *et al.* (1974) and that the *E. moebiusi* described by Curds (1974) conforms to the descriptions of Kahl (1932) and to the part of the silver-line system shown by Klein (1958).

DIAGNOSIS. *Euplotes rariseta* (Fig. 42) is a small (30–45 μm long, 20–31 μm wide) marine hypotrich with 10 frontoventral, 5 transverse and 3 caudal cirri. The cirrus below the AZM is stout. The ventral surface is heavily sculptured with 6 posteriorly projecting ridges. The dorsal surface has an argyrome of the double-patella type with 6 dorsolateral kineties carrying a maximum of 6 cilia in the mid-dorsal rows. The macronucleus is an irregular S-shape.

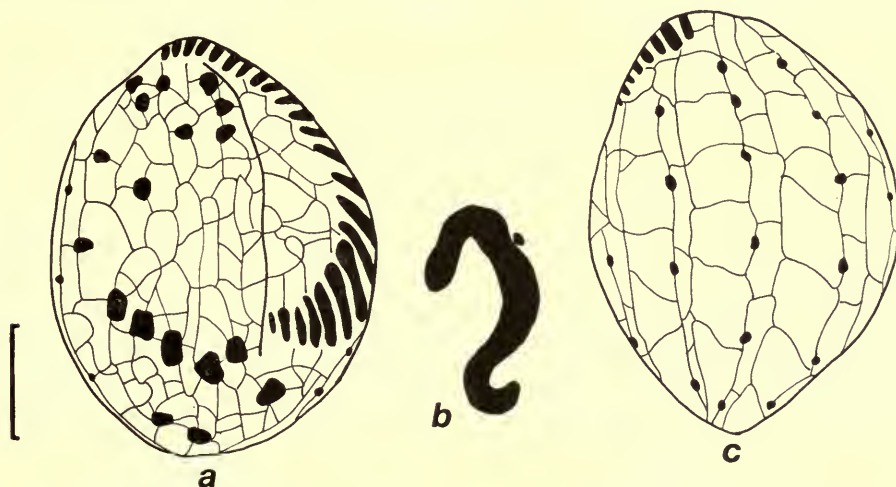


FIG. 42. *Euplotes rariseta*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome.
(After Curds, West & Dorahy, 1974.)

Euplotes strelkovi Agamaliyev, 1967

This species was described by Agamaliyev (1967) from samples of sand taken from the Caspian Sea.

DIAGNOSIS. *Euplotes strelkovi* (Fig. 43) is a small (50 μm long, 40 μm wide) marine species that is particularly round in outline shape. The peristome is of medium size and the right margin is essentially straight. The AZM extends about $\frac{3}{4}$ down the body and is composed of 33–38 membranelles. The dorsal argyrome is of the double-patella type with 6 dorsolateral kineties bearing up to 10 cilia in the mid-dorsal rows. The small polygons of the dorsal argyrome are on the left of the kineties. There are 8 frontoventral, a unique 6 transverse and 3 caudal cirri. The macronucleus is an irregular open C-shape with a compact micronucleus situated anteriorly.

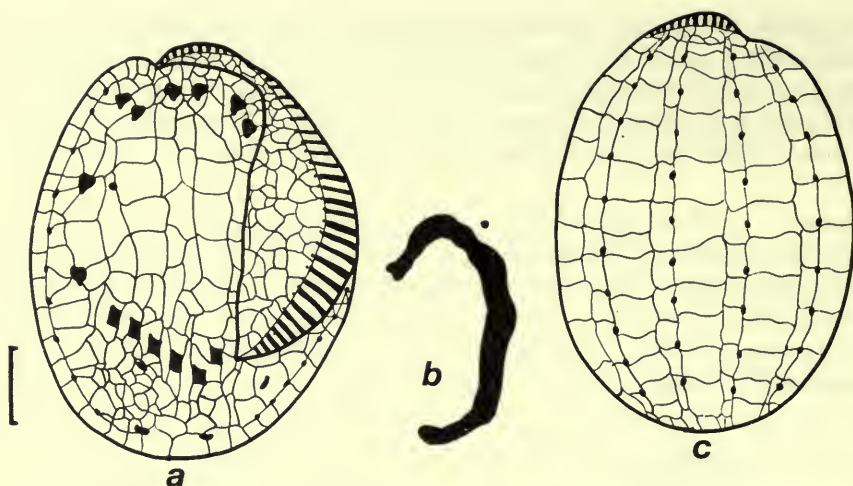


FIG. 43. *Euplotes strelkovi*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Agamaliyev, 1967.)

***Euplotes zenkewitchi* Burkovsky, 1970**

This species was first described by Burkovsky (1970) and more recently by Agamaliyev (1972).

DIAGNOSIS. *Euplotes zenkewitchi* (Fig. 44) is a medium (80 μm long, 50 μm wide) marine elongate hypotrich. The peristome is quite narrow and elongate extending just over halfway down the body. The AZM contains 50–55 membranelles. The dorsal argyrome is of the double-patella type except that the narrow polygons lie

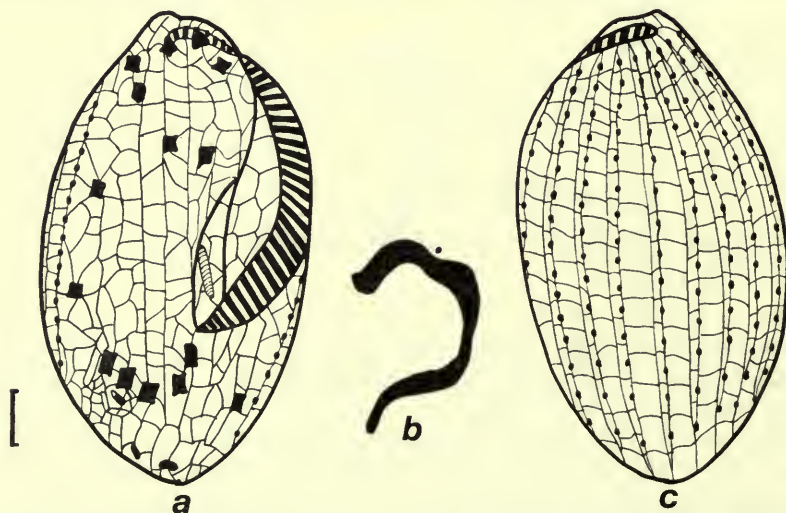


FIG. 44. *Euplotes zenkewitchi*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Burkovsky, 1970.)

on the left of the kineties. There are 10 dorsolateral kineties with up to 18 dorsal cilia in the central rows. There are 9 frontoventral, 5 transverse and 3 or 4 caudal cirri. The macronucleus is C-shaped with a posteriorly pointing tail. The micronucleus is in an anterior position.

SECTION D. KEY TO SPECIES WITH A MULTIPLE TYPE DORSAL ARGYROME

- 43 a** Polygons of dorsal argyrome approximately equal in shape and size, with 9 or 10 dorsolateral kineties **44**
b Polygons of dorsal argyrome of two types, squat polygons bordering the dorsal cilia and very long polygons between squat ones, with 6 dorsolateral kineties *E. tegulatus*
44 a 10 frontoventral cirri, 9 dorsolateral kineties with 11–20 dorsal cilia in central rows *E. indentatus*
b 9 frontoventral cirri, 10 dorsolateral kineties with over 30 dorsal cilia in central rows *E. muscicola*

SECTION D. DESCRIPTIONS OF SPECIES

Euplotes indentatus Carter, 1972

This species is a recent addition to the species of the genus and its description relies upon that of Carter (1972).

DIAGNOSIS. *Euplotes indentatus* (Fig. 45) is a small (60 μm long, 45 μm wide) marine species. The body is distinctly oval in outline shape with a prominent anterior notch in the upper border of the dorsal surface. The AZM is composed of 42–48 membranelles and extends $\frac{2}{3}$ of the body length. There are 10 frontoventral, 5 transverse and 4 caudal cirri. The dorsal surface is convex and deeply ridged.

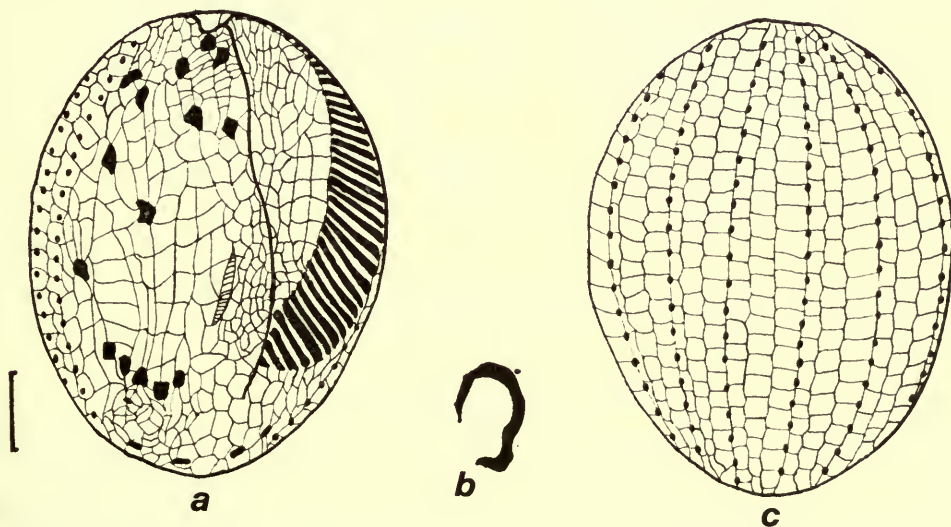


FIG. 45. *Euplotes indentatus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Carter, 1972.)

The dorsal argyrome is of the multiple type with three regular rows of polygons between the kineties. There are 9 dorsolateral kineties bearing a maximum of 15–21 cilia in the mid-dorsal rows. The macronucleus is a closed C-shape with the anterior micronucleus situated in a slight invagination.

Euplotes muscicola Kahl, 1932

Although this species was initially described by Kahl (1932) and its encystment by Fauré-Fremiet, Gauchery and Tuffrau (1954) a complete description was not available until Tuffrau (1960) published its silver-line system.

DIAGNOSIS. *Euplotes muscicola* (Fig. 46) is a medium (60–70 μm long) elongate oval freshwater hypotrich. The peristome is long and occupies about $\frac{3}{4}$ of the anterior left side of the ventral surface. The AZM contains about 35 membranelles. There are 9 frontoventral, 5 transverse and 4 caudal cirri. The dorsal argyrome is of the multiple type and consists of 4 regular rows of small polygons between the kineties. There are 10 dorsolateral kineties bearing up to about 35 cilia in the mid-dorsal rows. The macronucleus is an open C-shape with a compact micronucleus situated about halfway down its left side.

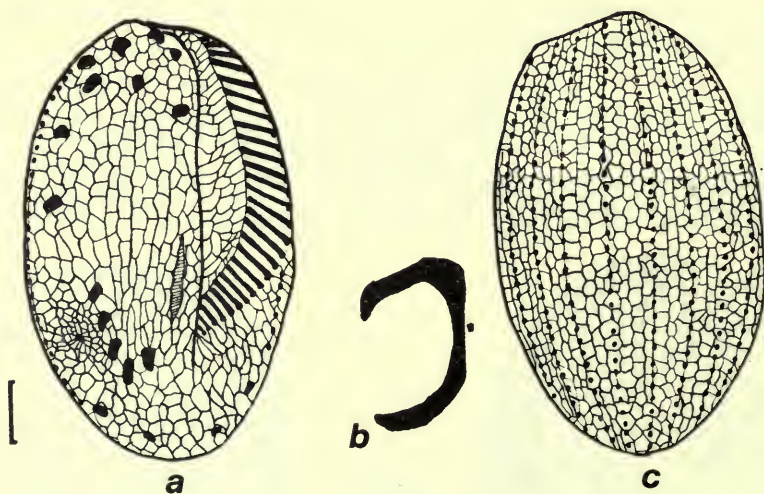


FIG. 46. *Euplotes muscicola*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

Euplotes tegulatus Tuffrau, 1960

The description of this species relies solely upon that of the original by Tuffrau (1960).

DIAGNOSIS. *Euplotes tegulatus* (Fig. 47) is a large (116 μm long) marine species that has an elongate ellipsoidal shape. The dorsal surface is prominently sculptured with 3 or 4 ridges. The ventral surface has a pronounced longitudinal ridge that

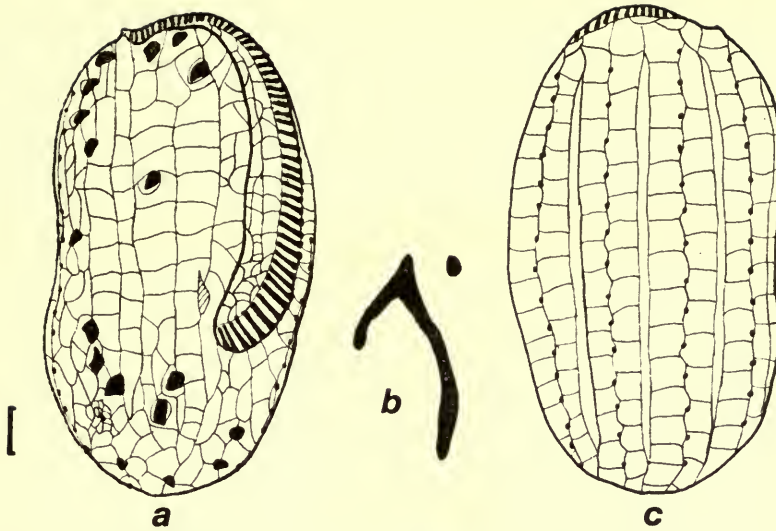


FIG. 47. *Euplotes tegulatus*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome.
(After Tuffrau, 1960.)

ends both posteriorly and anteriorly in spines. The anterior ventral spine is short but projects forward beyond the margin of the body. The peristome is long and curved extending down $\frac{2}{3}$ of the body length. The AZM consists of about 55 membranelles. The dorsal argyrome is of the multiple type but is unique in that there are two longitudinal fibrils between the dorsolateral fibrils. There are 6 dorsolateral kineties with up to 15 cilia in the mid-dorsal rows. There are 9 frontoventral, 5 transverse and 4 caudal cirri. The macronucleus is highly angular in appearance; it is composed of two arms joined anteriorly at an acute angle. The micronucleus is very large for the genus (7–8 μm diameter) and is situated anteriorly on the left of the macronucleus.

SECTION E. KEY TO SPECIES WITH A COMPLEX TYPE DORSAL ARGYROME

- | | | | |
|--|---|---------------------|--|
| 45 a | 10 frontoventral cirri | 46 | |
| b | 9 frontoventral cirri | 47 | |
| 46 a | 7 dorsolateral kineties, complex dorsal argyrome network interspersed with regular rows of polygons | <i>E. moebiusi</i> | |
| b | 11 dorsolateral kineties, complex dorsal argyrome network complete or partially so | <i>E. mutabilis</i> | |
| (N.B. This species is undergoing reorganization – its description is given in Section A, p. 14.) | | | |
| 47 a | 7 dorsolateral kineties with 11–15 cilia in mid-dorsal rows | <i>E. gracilis</i> | |
| b | 8 dorsolateral kineties with 20 or more cilia in mid-dorsal rows | 48 | |
| 48 a | 20–25 dorsal cilia in central kineties, AZM with 30–35 membranelles | <i>E. muscorum</i> | |
| b | More than 25 (usually 25–45) cilia in mid-dorsal kineties, AZM with 40–45 membranelles | <i>E. elegans</i> | |

SECTION E. DESCRIPTIONS OF THE SPECIES

Euplotes elegans Kahl, 1932

This species was originally described briefly by Kahl (1932) and then redescribed in detail by both Tuffrau (1960) and Carter (1972). Kahl (1932) and Dragesco (1960) have also described a form of this species, *E. elegans* forma *littoralis*, but this differs little from *E. elegans* and such a differentiation does not appear to be warranted.

DIAGNOSIS. *Euplotes elegans* (Fig. 48) is a medium (80 μm long, 55 μm wide) euryhaline species that has an oval outline shape. The peristome is large and extends about $\frac{3}{4}$ down the length of the body. The AZM is composed of 40–45 strong membranelles. There are 9 frontoventral, 5 transverse and 3 or 4 caudal cirri. The original description by Kahl (1932) appears to be the only observation of the presence of 3 caudal cirri. The dorsal argyrome is of the complex type consisting of many irregular polygons. There are 8 dorsolateral kineties with a maximum of 30–46 dorsal cilia in the central kineties. The left lateral kinety is short with only 4–8 cilia and is easily overlooked. The macronucleus is C-shaped with a small, blunt, knob-like projection on the upper arm and both arms taper to points. The micronucleus is small and compact.

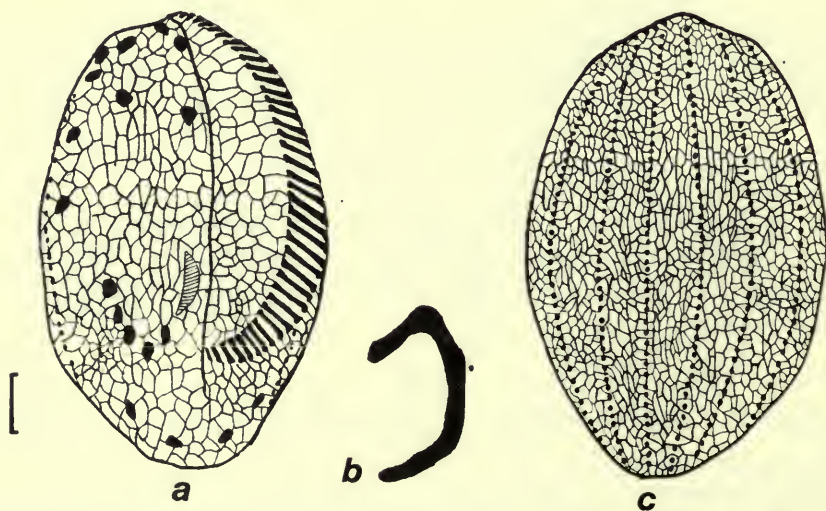


FIG. 48. *Euplotes elegans*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

Euplotes gracilis Kahl, 1932

First briefly described by Kahl (1932) this species was more fully described by Tuffrau (1960).

DIAGNOSIS. *Euplotes gracilis* (Fig. 49) is a small (37–50 μm long) freshwater species that has an elongate oval shape. The peristome is very deep and extends

about $\frac{3}{4}$ down the length of the body. The AZM is composed of 30–35 membranelles. There are 9 frontoventral, 5 transverse and 4 caudal cirri. The frontoventral cirri are very long and styliform whereas the caudals are thin. The dorsal argyrome is of a complex nature consisting of an irregular assemblage of polygons between the 7 dorsolateral kineties. There are 10–13 large kinetosomes in the mid-dorsal kineties. The macronucleus is C-shaped and the micronucleus is situated approximately $\frac{1}{3}$ of the way down its left edge.

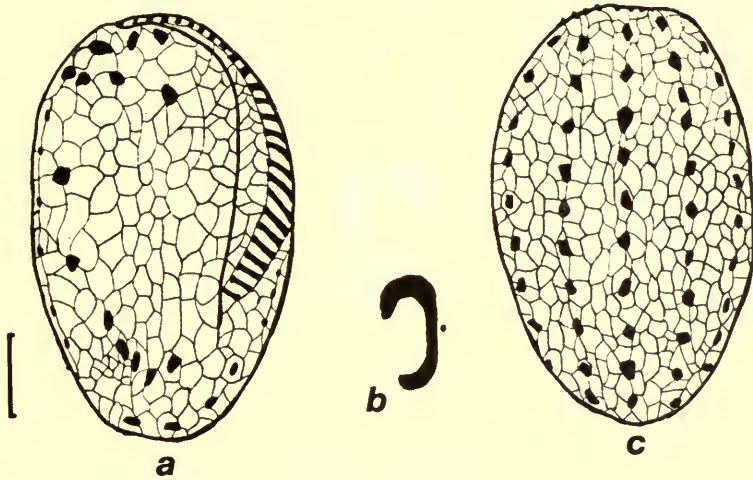


FIG. 49. *Euplotes gracilis*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Tuffrau, 1960.)

Euplotes moebiusi Kahl, 1932

Until recently *E. moebiusi* could only be identified from the brief and incomplete descriptions of Kahl (1932). Borror (1963) described an organism as *E. moebiusi* but this was later shown by Curds, West and Dorahy (1974) to be a new species, *E. rariseta*. Photographs of part of the silver-line system were first published by Klein (1958) in order to demonstrate the 'dry' silver method and although these were not sufficiently comprehensive for identification purposes they do conform with the silver-line systems described by Curds (1974). Tuffrau (1960) considered *E. moebiusi* to be a synonym of *E. charon* Ehrenberg, 1830.

DIAGNOSIS. *Euplotes moebiusi* (Fig. 50) is a medium (60 μm long, 40 μm wide), ovoid euryhaline hypotrich with 10 frontoventral, 5 transverse and 4 caudal cirri. The ventral surface is heavily sculptured with 7 ridges and the dorsal surface with 5 longitudinal ridges. The AZM is composed of 35–40 membranelles which extend $\frac{3}{4}$ the length of the cell. The dorsal argyrome is unique amongst those species described to date; there are 5 longitudinal rows of narrow polygons interspersed with an irregular network of larger polygons. The presence of the irregular network has been thought to be sufficient to place it within the 'complex' group until data

concerning other species become available. There are 7 dorsolateral kineties bearing a maximum of 11 cilia in the mid-dorsal rows. The macronucleus is 3-shaped and the micronucleus is situated anteriorly.

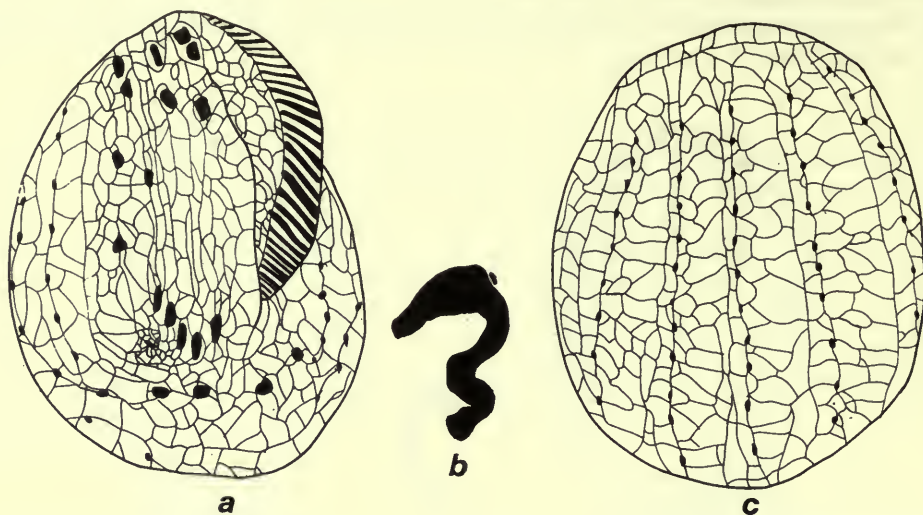


FIG. 50. *Euplotes moebiusi*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Curds, 1974.)

Euplotes muscorum Dragesco, 1970

This species was isolated from samples of moss collected in Africa by Dragesco (1970).

DIAGNOSIS. *Euplotes muscorum* (Fig. 51) is a small to medium (50–70 μm long) elongate freshwater species. The AZM contains approximately 30 membranelles and extends about $\frac{2}{3}$ down the body. There are 9 frontoventral, 5 transverse and 4 long caudal cirri. The dorsal argyrome is of the complex type with many polygons arranged irregularly between the kineties. There are 8 dorsolateral kineties carrying 22–28 cilia in the mid-dorsal rows on the peaks of the longitudinal ridges. The macronucleus is C-shaped with the pointed right arm projecting posteriorly over halfway down the length of the body. The micronucleus is situated anteriorly almost in line with the central longitudinal axis of the body.

SECTION F. UNDEFINED SPECIES

The silver-line systems of the following seven recognizable species have not yet been described. Their descriptions are given in alphabetical order.

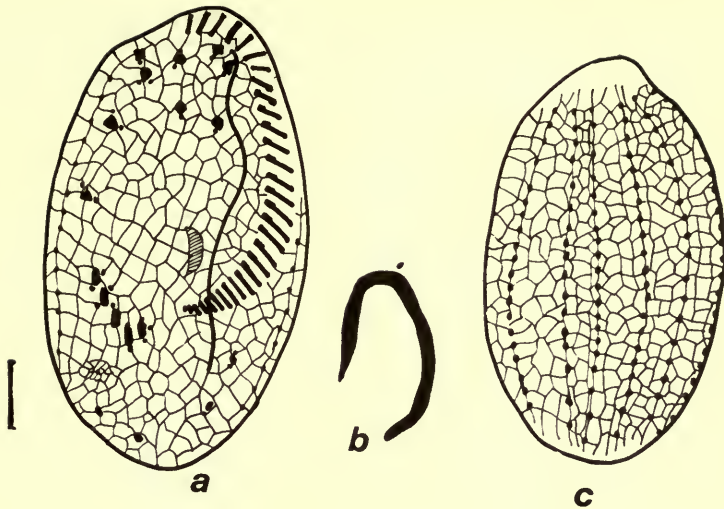


FIG. 51. *Euplotes muscorum*. a. Ventral argyrome. b. Nuclei. c. Dorsal argyrome. (After Dragesco, 1970.)

Euplotes aberrans Dragesco, 1960

This species was briefly and inadequately described by Dragesco (1960) from samples of marine sands but for several reasons may be regarded as a distinct species until further data are gathered.

DIAGNOSIS. *Euplotes aberrans* (Fig. 52) is a medium (70–80 μm long) marine ciliate whose shape is highly elongate. There is a distinct spike-like projection on the right of the peristomial collar. The dorsal surface bears 4 pronounced ridges and there are 2 major ones, amongst others, on the ventral surface which travel slightly transversally almost the entire length of the body. The peristome is long and narrow extending about $\frac{2}{3}$ down the body and is composed of about 50 membranelles. There are 8 frontoventral cirri which is a feature shared by only three other species (*E. strelkovi*, *E. raikovi* and *E. poljanskyi* – all of which have differently shaped macronuclei). There are 5 transverse cirri in two groups and 4 caudals. There is a very large subequatorial vacuole which has not yet been seen to contract. The macronucleus is horseshoe shaped whose ends almost meet one another. The micronucleus lies within a definite indentation in the anterior of the macronucleus.

Euplotes novemcarinata Wang, 1930

Recognition of this species relies upon the single description by Wang (1930).

DIAGNOSIS. *Euplotes novemcarinata* (Fig. 53) is a small to medium (60–75 μm long) freshwater ciliate whose deep ridges are distinctive. The overall outline shape of the body is oval but there is a wing-like extension on the left side due to the projection of one of the ridges. There are 9 longitudinal ridges, 5 are dorsal, 1 lateral and

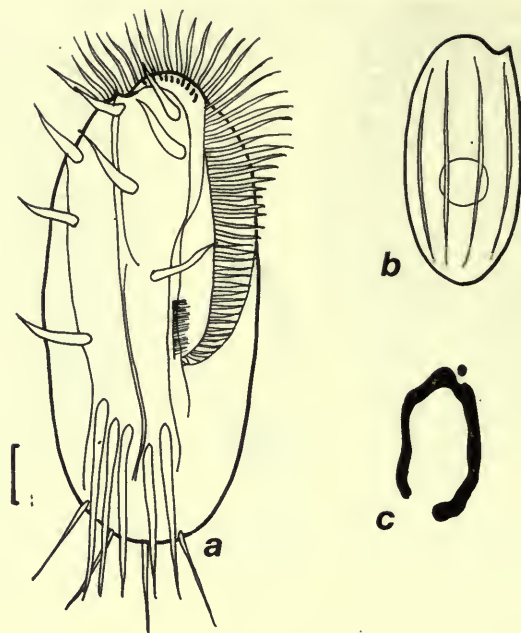


FIG. 52. *Euplotes aberrans*. a. Ventral aspect. b. Dorsal aspect. c. Nuclei.
(After Dragesco, 1960.)

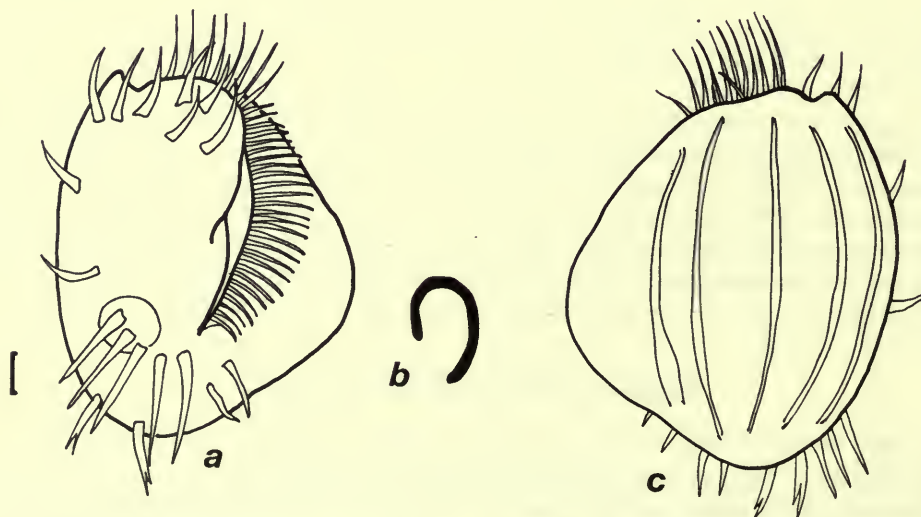


FIG. 53. *Euplotes novemcarinata*. a. Ventral aspect. b. Macronucleus. c. Dorsal aspect.
(After Wang, 1930.)

3 less prominent ones are restricted to the ventral surface. The anterior end of the body has a concave notch and the peristome extends down $\frac{2}{3}$ of the body length. There are 9 frontoventral, 5 transverse and 4 caudal cirri. The macronucleus is C-shaped.

Euplotes roscoffensis Dragesco, 1966

Although this species was not described until 1966 it was in fact first studied in 1950 long before the importance of silver preparations for *Euplotes* taxonomy was realized. However, because the right-hand border of the peristome is so distinctive this should be an easily identifiable species.

DIAGNOSIS. *Euplotes roscoffensis* (Fig. 54) is a small to medium (60–70 μm long) ovoid marine ciliate. The right border of the peristome is straight until it reaches the level of the undulating membrane just below the middle of the cell, here the peristome border bears a distinctive deep invagination or pocket (Fig. 53) which appears to be a unique character. The AZM is composed of 40–50 membranelles. There are 10 frontoventral, 5 transverse and 4 caudal cirri. The large contractile vacuole which is situated in the proximity of transverse cirrus VI 1 often has several small satellite vacuoles surrounding it. The macronucleus is C-shaped with a club-like structure at the posterior end. The micronucleus is small, round and situated close to the anterior left edge of the macronucleus.

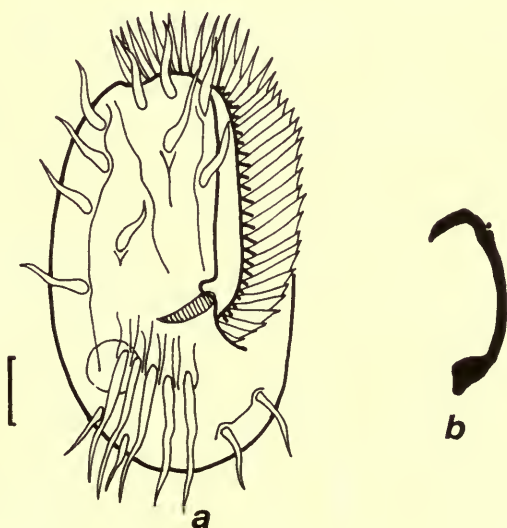


FIG. 54. *Euplotes roscoffensis*. a. Ventral aspect. b. Nuclei. (After Dragesco, 1966.)

Euplotes rotunda Gelei, 1950

The identity of this species relies upon the single brief and inadequate description of Gelei (1950).

DIAGNOSIS. *Euplotes rotunda* (Fig. 55) is a small (50 μm long, 40 μm wide) round freshwater species. The peristome extends down to about the centre of the body and the AZM carries approximately 25 membranelles. There are 8 dorsolateral kineties with about 10 cilia in the mid-dorsal rows. There are 9 frontoventral, 5 transverse and 3 caudal cirri. The macronucleus is a flattened 3-shape.

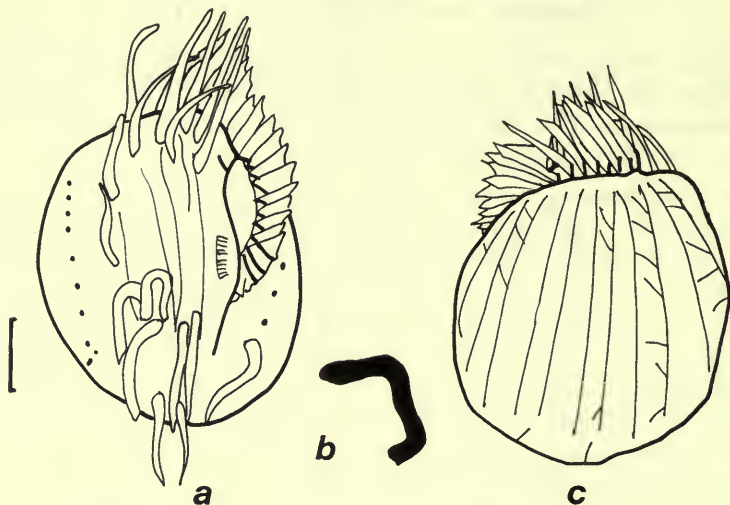


FIG. 55. *Euplotes rotunda*. a. Ventral aspect. b. Macronucleus. c. Dorsal aspect. (After Gelei, 1950.)

Euplotes terricola Penard, 1922

This species relies upon the single description by Penard (1922) who found it in samples of moss. Tuffrau (1960) was unconvinced that this organism is in fact a member of the genus but both Kahl (1932) and Borror (1972) include it in their works.

DIAGNOSIS. *Euplotes terricola* (Fig. 56) is a small to medium (60–65 μm long) freshwater species that is generally oval in outline but tends to narrow posteriorly to a blunt point. The peristome is relatively short and extends just to the centre of the body and there appear to be somewhere in the order of 20 membranelles in the AZM. The dorsal surface seems to have 6 ridges and there are 9 frontoventral and 5 transverse cirri. According to Kahl (1932), there are 10 caudal cirri although Penard (1922) originally described these as being very fine marginal cirri. The macronucleus is a simple hoop-shape but the micronucleus is illustrated as lying inside the curve of the macronucleus which is an unusual feature for the genus. It is apparent that there are many doubts about this organism and it requires redescription before it can be adequately assessed.

Euplotes thononensis Dragesco, 1960

Recognition of this organism relies upon the brief and inadequate description by Dragesco (1960).

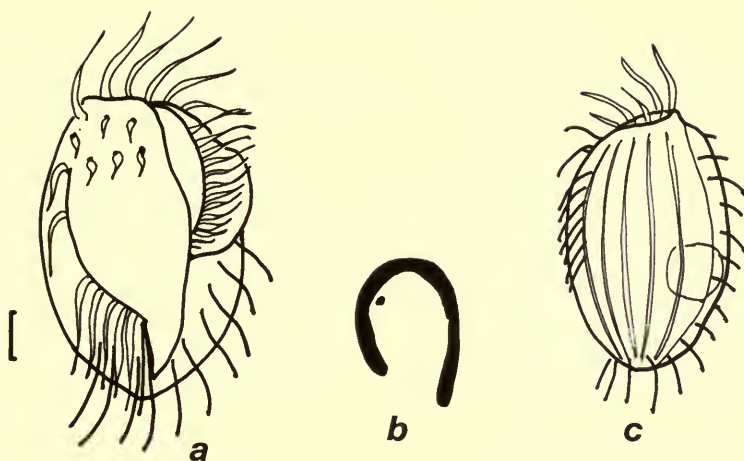


FIG. 56. *Euplotes terricola*. a. Ventral aspect. b. Nuclei. c. Dorsal aspect.
(After Penard, 1922.)

DIAGNOSIS. *Euplotes thononensis* (Fig. 57) is a medium to large (90 μm long) marine species whose outline shape is oval except for the pronounced projecting peristomial collar. The dorsal surface carries 12 longitudinal furrows and there appear to be about 11 dorsal cilia. The peristome is wide but extends less than half-way down the cell. There are 9 frontoventral cirri, one of which originates on the peristome border beneath the peristomial collar. There are 5 transverse and 4 caudal cirri. A group of 3 contractile vacuoles is positioned close to the transverse cirri. The macronucleus is an open C-shape with the micronucleus in an anterior position.

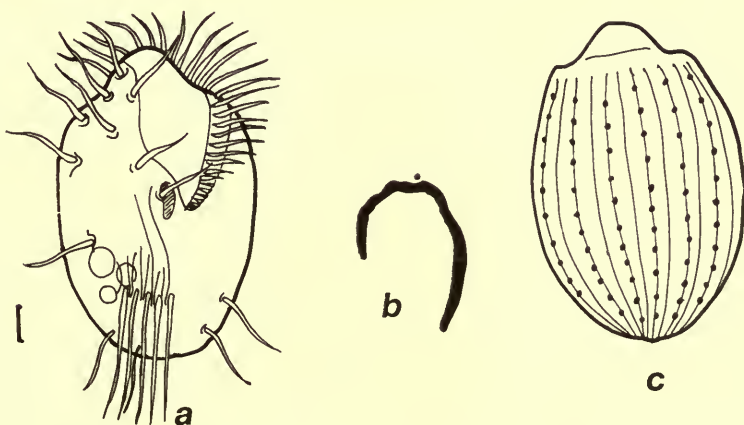


FIG. 57. *Euplotes thononensis*. a. Ventral aspect. b. Nuclei. c. Dorsal aspect.
(After Dragesco, 1960.)

Euplotes woodruffi Gaw, 1939

This species was first described by Gaw (1939) and more recently by Borror (1963). Unfortunately its silver-line system is still unknown but its unique macronucleus enables it to be easily recognized.

DIAGNOSIS. *Euplotes woodruffi* (Fig. 58) is a large (145 μm long) euryhaline oval species with a well-defined peristomial collar. The peristome is large, triangular in shape and extends about $\frac{2}{3}$ of the way down the body. The AZM is composed of 60–70 membranelles. The dorsal surface is sculptured with 8–10 grooves and there are 8 dorsolateral kineties with about 60 closely set cilia in the central rows. There are 9 frontoventral, 5 transverse and 4 caudal cirri. The unique macronucleus is T- or Y-shaped with the micronucleus in an anterior position.

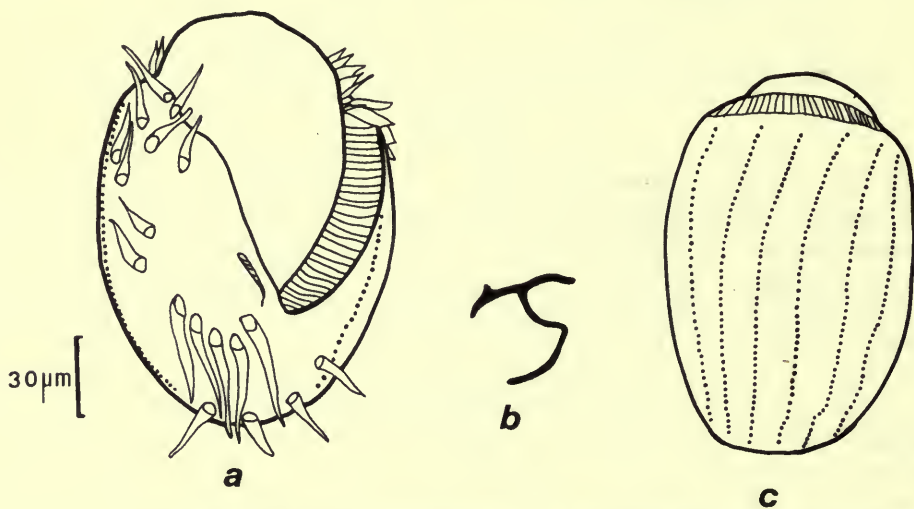


FIG. 58. *Euplotes woodruffi*. a. Ventral aspect. b. Macronucleus. c. Dorsal aspect. (After Borror, 1963.)

APPENDIX I CHECK-LIST AND INDEX OF SPECIES AND SYNONYMS

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- | | | | |
|--|----|---|----|
| 36. <i>Euplotes poljanskyi</i> Agamaliiev, 1966 | 34 | 49. <i>Euplotes vannus</i> (cont.) | |
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| <i>Euplotes moebiusi</i> Borrer, 1963 | | mann, 1858 | |
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| 48. <i>Euplotes tuffraui</i> Berger, 1965 | 37 | 1886 | |
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Addendum

Since the preparation of this manuscript it has been brought to the author's notice that a silver-line preparation of *E. woodruffi* has been published (Magagnini & Nobili, 1964). It is of the double-eurystomus type with 8 dorsolateral kineties and 25 middorsal cilia. In the existing key these characters would lead to *E. aediculatus* and *N. eurystomus*. All three species may be easily distinguished by their nuclear features.

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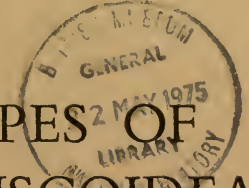
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CATALOGUE OF THE TYPES OF
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IN THE COLLECTIONS OF THE
BRITISH MUSEUM (NATURAL HISTORY)
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PSEUDOTRACHEATA

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By JOAN P. ELLIS AND ROGER J. LINCOLN

THE following list incorporates all the families of woodlice represented in the Museum collection of types with the exception of the pseudotracheate group which are listed in Part I of the type-catalogue (Lincoln & Ellis, 1974). Part II comprises 429 separate items referring to 245 species and 76 genera within the following families: Tylidae, Styloniscidae, Titaniidae, Schobliidae, Trichoniscidae, Buddelundiellidae, Ligiidae, Stenoniscidae, Tendosphaeridae, Squamiferidae and Oniscidae.

The style and arrangement of this catalogue are similar to Part I, and a list of the manuscript names referred to in the Appendix has been deposited in the library of the British Museum (Natural History).

In total, this impressive collection of woodlice type material has over 1100 registered entries representing 767 species in 153 different genera, and is thus of considerable significance in a group which has only about 300 genera and rather more than 2000 recognized species (Vandel, 1960).

Family TYLIDAE

TYLOS Latreille

granuliferus Budde-Lund (1885 : 279) [Nom. nov. for *Tylos granulatus* Miers (1877 : 674)]

SYNTYPES : two females, plus one specimen without abdomen (dry). Reg. no. 1847:21. Borneo ; 'among rotten woods, forest of Borneo, Eastern Seas'. Collected by Arthur Adams, H.M.S. 'Samarang'. Presented by Capt. Sir E. Belcher.

SYNTYPE : female. Reg. no. 1872:17. Hiogo, Japan. Collected by George Lewis. Presented by F. Smith.

neozelandicus Chilton (1901 : 120)

SYNTYPE (?) : female. Reg. no. 1900:11:1:55. Wellington, New Zealand. Presented by C. Chilton.

niveus Budde-Lund (1885 : 278)

SYNTYPES (?) : one male ; one female ; one damaged specimen. (The description states 'two examples'.) Reg. no. 1921:10:18:693-696. Key West, Florida, USA. 1878. Budde-Lund Collection.

nudulus Budde-Lund (1906 : 76)

SYNTYPES : one male ; one female. Reg. no. 1902:12:4:4-5. Christmas I. December 1897 ; 'under stones and rotten wood'. Presented by J. Murray.

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:697-699. Christmas I. Budde-Lund Collection.

opercularis Budde-Lund (1885 : 277)

SYNTYPE : one specimen in fragments. Reg. no. 1921:10:18:700. Philippine Is. Collected by Cumming. Budde-Lund Collection.

ponticus Budde-Lund (1885 : 274)

SYNTYPES : two females. Reg. no. 1921:10:18:701-702. Sevastopol, Ukraine, USSR. Collected by Grebnitzky. Budde-Lund Collection (ex Uljanin Collection).

Family **STYLONISCIDAE*****CLAVIGERONISCUS*** Arcangeli***mussau*** Vandel (1973 : 20)

SYNTYPES : thirty-five specimens : males, females and juveniles. Reg. no. 1970:343:35. Near Kuzi, Kolombangara, Solomon Is. 3-9.9.1965. 250-500 ft ; 'forest litter'. Collected by P. N. Lawrence and Isiah. Presented by the Royal Society.

SYNTYPES : thirty-six specimens : males, females and juveniles. Reg. no. 1970:344:36. Near Kuzi, Kolombangara, Solomon Is. 8.9.1965. 50 ft ; 'valley litter'. Collected by P. N. Lawrence and Isiah. Presented by the Royal Society.

SYNTYPES : one male ; three females ; one juvenile. Reg. no. 1970:345:9. N. of Kiai, Kolombangara, Solomon Is. 6.9.1965. 1000 ft ; 'forest litter'. Collected by P. N. Lawrence and Isiah. Presented by the Royal Society.

SYNTYPES : three females. Reg. no. 1970:346:3. S.E. San Jorge, S. of Santa Isabel, Solomon Is. 23.9.1965 ; 'rotten wood litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : four females. Reg. no. 1970:347:4. Fulakora Pt, Raja, Santa Isabel, Solomon Is. 30.9.1965 ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : two males ; nine females ; one juvenile. Reg. no. 1970:348:12. Lilihinia I., Santa Isabel, Solomon Is. 21.9.1965 ; 'shore litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : one male ; eleven females. Reg. no. 1970:349:12. Cockatoo I., Santa Isabel, Solomon Is. 19-20.9.1965 ; 'shore litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE : male. Reg. no. 1970:350:1. Thousand Ships Bay, opposite Lilihinia I., Santa Isabel, Solomon Is. 20.9.1965 ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : male ; nine females. Reg. no. 1970:351:10. E. central San Jorge I., S. of Santa Isabel, Solomon Is. 24.9.1965 ; 'forest litter'. Collected by J. Peake and P. N. Lawrence. Presented by the Royal Society.

SYNTYPE : female. Reg. no. 1970:352:1. S. of San Jorge, Santa Isabel, Solomon Is. 22.9.1965 ; 'gully litter'. Collected by J. Peake and P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : twenty-eight specimens : males, females and juveniles. Reg. no. 1970:353:28. Popamanisiu, Guadalcanal, Solomon Is. 1965. 4400-7000 ft. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : twenty-one specimens : males and females. Reg. no. 1970:354:21. Mt Gallago, Guadalcanal, Solomon Is. 12.7.1965. 2500-3600 ft. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : two females. Reg. no. 1970:355:10 (part). Monitor Creek, Umasani River, Guadalcanal, Solomon Is. 8.7.1965 ; 'forest litter in hollow'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; seven females. Reg. no. 1970:355:10 (part). Umasani River, nr Mt Gallego, c. 6 miles S.W. Tamboko, Guadalcanal, Solomon Is. 4.7.1965; 'disturbed forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: forty-two specimens: males, females and juveniles. Reg. no. 1970:356:42. Mt Austin, nr Honiara, Guadalcanal, Solomon Is. 24.7.1965. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two females. Reg. no. 1970:357:2. Nuhu, Guadalcanal, Solomon Is. 28-31.10.1965. 1000 ft; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: thirty-six specimens: males, females and juveniles. Reg. no. 1970:358:36. Environs of Wainoni, San Cristobal, Solomon Is. 1965. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: forty specimens: males, females and juveniles. Reg. no. 1970:359:40. Confluence of Warahito and Pagato Rivers, San Cristobal, Solomon Is. 1965. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two males; eight females. Reg. no. 1970:360:10. Huni River estuary, c. N.E. Wainoni, San Cristobal, Solomon Is. 9-12.8.1965; 'forest litter coral limestone'. Collected by Isiah. Presented by the Royal Society.

SYNTYPES: three males; fourteen females. Reg. no. 1970:361:17. Ngaliau Hill, Pawa, Ugi, Solomon Is. 20.7.1965; 'secondary forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

CORDIONISCUS Graeve

spinosus (Patience) (1907a : 85) [*Trichoniscus spinosus*]

SYNTYPES: one male; three females. Reg. no. 1907:5:29:6-9. Springburn Public Park, Glasgow, Scotland; 'in greenhouse'. Presented and collected by A. Patience.

SYNTYPES: four females. Reg. no. 1911:11:8:10984-89. Springburn Public Park, Glasgow, Scotland. 1907; 'in greenhouse'. Collected by A. Patience. A. M. Norman Collection (ex Patience Collection).

stebbingi (Patience) (1907b : 42) [*Trichoniscus stebbingi*]

SYNTYPES: two males; three females. Reg. no. 1907:5:29:1-5. Springburn Public Park, Glasgow, Scotland. Presented and collected by A. Patience.

SYNTYPES: two males; one female. Reg. no. 1911:11:8:10979-81. Scotland; Hawkshead Asylum, Renfrewshire, and Glasgow; 'in greenhouses'. A. M. Norman Collection.

SYNTYPES: three males. Reg. no. 1921:10:18:250-253. Glasgow, Scotland. Collected by A. Patience. Budde-Lund Collection (ex Patience Collection).

INDONISCUS Vandel

orientalis Vandel (1973 : 18)

SYNTYPES: one female; one damaged specimen. Reg. no. 1970:432:6 (part). Popamanisiu, Guadalcanal I., Solomon Is. 1-4.11.1965. 4400 ft; 'mossy ridge forest litter'. Collected by P. N. Lawrence and Isiah. Presented by the Royal Society.

SYNTYPES: one female; one juvenile. Reg. no. 1970:432:6 (part). Popamanisiu, Guadalcanal I., Solomon Is. 5.11.1965. 7000 ft; 'bog masses around trees'. Collected by P. N. Lawrence and Isiah. Presented by the Royal Society.

SYNTYPES: three females. Reg. no. 1970:432:6 (part). Popamanisiu, Guadalcanal I., Solomon Is. 6.11.1965. 7000 ft; 'moss forest'. Collected by P. N. Lawrence and Isiah. Presented by the Royal Society.

SYNTYPE: male. Reg. no. 1970:433:1. S.E. Wainoni, San Cristobal, Solomon Is. 10.8.1965. 1650 ft; 'moss forest'. Collected by P. N. Lawrence and Isiah. Presented by the Royal Society.

PARANOTONISCUS Barnard**capensis** Barnard (1932 : 202)

SYNTYPES : three males ; two females. Reg. no. 1933:1:25:934-939. Table Mt, Cape Province, S. Africa. 2000-3000 ft. Collected and presented by K. H. Barnard.

latus Barnard (1932 : 205)

SYNTYPES : three females. Reg. no. 1933:1:25:940-942. River Zonder End Mts, Cape Province, S. Africa. Collected and presented by K. H. Barnard.

montanus Barnard (1932 : 204)

SYNTYPES : three males ; seven females. Reg. no. 1933:1:25:943-950. Hottentots Holland Mts, Cape Province, S. Africa. 1916. 4000 ft. Barnard Collection.

ornatus Barnard (1932 : 205)

SYNTYPES : approx. seven specimens in fragments, mainly ovigerous females. Reg. no. 1933:1:25:951-956. Wellington Mts, Cape Province, S. Africa. 2000-3500 ft. Collected and presented by K. H. Barnard.

tuberculatus Barnard (1932 : 204)

SYNTYPE : male. Reg. no. 1933:1:25:957. Langeberg Range, Cape Province, S. Africa. 1927. 2000 ft. Collected and presented by K. H. Barnard.

STYLONISCUS Dana**australis** (Dollfus) (1890 : 6) [*Trichoniscus australis*]

HOLOTYPE : female. Reg. no. 1927:5:14:40. Inaccessible I., Tristan d'Acunha. 16.10.1873. 'Challenger' Collection.

austroafricanus (Barnard) (1932 : 200) [*Trichoniscus austroafricanus*]

SYNTYPES : one male ; one female. Reg. no. 1933:1:25:903-904. Table Mt, Cape Province, S. Africa. Collected and presented by K. H. Barnard.

cestus (Barnard) (1932 : 201) [*Trichoniscus cestus*]

SYNTYPES : seven females. Reg. no. 1933:1:25:905-910. Riversdale Mts, Cape Province, S. Africa. 1926. Collected and presented by K. H. Barnard.

georgensis (Barnard) (1932 : 200) [*Trichoniscus georgensis*]

SYNTYPES : two females. Reg. no. 1933:1:25:911-912. George, Cape Province, S. Africa. 1931. Collected and presented by K. H. Barnard.

horae (Barnard) (1932 : 200) [*Trichoniscus horae*]

SYNTYPES : four females. Reg. no. 1933:1:25:915-917. Swellendam Mts, Cape Province, S. Africa. 1925. Collected and presented by K. H. Barnard.

hottentoti (Barnard) (1932 : 197) [*Trichoniscus hottentoti*]

SYNTYPES : two females. Reg. no. 1933:1:25:913-914. Hottentots Holland Mts, Cape Province, S. Africa. 1916. Collected and presented by K. H. Barnard.

kermadecensis (Chilton) (1911 : 569) [*Trichoniscus kermadecensis*]

SYNTYPES : two females. Reg. no. 1912:5:25:67-68. Sunday I., Kermadec Is. 1908. Collected by W. R. B. Oliver. Presented by C. Chilton.

mauritiensis (Barnard) (1936 : 3) [*Trichoniscus mauritiensis*]

SYNTYPES : four males ; eleven females. Reg. no. 1936:7:13:1-5. Curepipe, Mauritius. 12.1.1935. Collected and presented by R. F. Lawrence.

monocellatus (Dollfus) (1890 : 7) [*Microniscus monocellatus*]

HOLOTYPE : male. Reg. no. 1927:5:14:41. Juan Fernandez beach. 'Challenger' Collection.

moruliceps (Barnard) (1932 : 199) [*Trichoniscus moruliceps*]

HOLOTYPE : female (many appendages missing). Reg. no. 1933:1:25:958. Jonkershoek Mts, Stellenbosch, Cape Province, S. Africa. 1924. Collected and presented by K. H. Barnard.

murrayi (Dollfus) (1890 : 5) [*Trichoniscus murrayi*]

HOLOTYPE : male. Reg. no. 1927:5:14:39. Valparaiso, Chile. November 1875. 'Challenger' Collection.

otakensis (Chilton) (1901 : 117) [*Trichoniscus otakensis*]

SYNTYPES : eight females. Reg. no. 1900:11:1:27-32. Dunedin, New Zealand. Presented by C. Chilton.

phormianus (Chilton) (1901 : 115) [*Trichoniscus phormianus*]

SYNTYPES : nine females. Reg. no. 1900:11:1:1-5. Canterbury, New Zealand. Presented by C. Chilton.

SYNTYPES (?) : two males ; two females. Reg. no. 1921:10:18:414-417. Canterbury, New Zealand. Budde-Lund Collection (ex Dundee University Collection).

riversdalei (Barnard) (1932 : 201) [*Trichoniscus riversdalei*]

SYNTYPE : male. Reg. no. 1933:1:25:926. Riversdale Mts, Cape Province, S. Africa. 1926. Collected and presented by K. H. Barnard.

swellendami (Barnard) (1932 : 201) [*Trichoniscus swellendami*]

SYNTYPES : two females. Reg. no. 1933:1:25:927-928. Swellendam, Cape Province, S. Africa. 1925. K. H. Barnard Collection.

tabulae (Barnard) (1932 : 195) [*Trichoniscus tabulae*]

SYNTYPES : four males ; three females. Reg. no. 1933:1:25:30-36. Table Mt, Cape Province, S. Africa. Collected and presented by K. H. Barnard.

ventosus (Barnard) (1932 : 199) [*Trichoniscus ventosus*]

SYNTYPES : three males ; two females. Reg. no. 1933:1:25:929-933. Waaihoek Mts, Goudini, Worcester District, Cape Province, S. Africa. 1928. Collected and presented by K. H. Barnard.

verrucosus (Budde-Lund) (1906 : 79) [*Trichoniscus verrucosus*]

SYNTYPES : thirty-four specimens : males, females and juveniles. Reg. no. 1921:10:18:422-433. Possession I. 25.12.1901. Budde-Lund Collection.

Family TITANIIDAE

KOGMANIA Barnard**depressa** Barnard (1932 : 209)

SYNTYPES : one male ; one female. Reg. no. 1933:1:25:44-45. Kogmans Kloof, Montagu, Cape Province, S. Africa. 1922. Presented and collected by K. H. Barnard.

Family SCHOBLIIDAE

SCHOBLIA Budde-Lund**circularis** Budde-Lund (1909 : 66)

SYNTYPE : few fragments only. Reg. no. 1921:10:18:451. East Africa. Budde-Lund Collection.

Family TRICHONISCIDAE

ALPIONISCUS Racovitza**fragilis** Budde-Lund (1909 : 68)

SYNTYPES : two males. Reg. no. 1921:10:18:571-572. Sardinia. Budde-Lund Collection.

Subgenus *ILLYRIONETHES* Verhoeff*heroldi* Verhoeff (1931b : 22)

HOLOTYPE : male. Reg. no. 1931:4:27:73. Hercegovini, Yugoslavia. Verhoeff Collection.

strasseri (Verhoeff) (1927b : 270)

SYNTYPE : male. Reg. no. 1928:7:4:55. Istrien, Italy. Collected by K. Strasser. Verhoeff Collection.

SYNTYPES : three males ; one female. Reg. no. 1930:5:26:76-79. Istrien, Italy. Collected by K. Strasser. Verhoeff Collection.

SYNTYPES : three males ; one female. Reg. no. 1937:7:6:132-135. Istrien, Italy. Collected by K. Strasser. Verhoeff Collection.

ANDRONISCUS Verhoeff*alpinus* Verhoeff (1908c : 140, 143)

SYNTYPE : female. Reg. no. 1908:6:1:30. Lugano, Italy. Verhoeff Collection.

brentanus Verhoeff (1932 : 22)

SYNTYPES : one male ; two females. Reg. no. 1937:7:6:57-59. Brenta, Italy. Collected by K. Strasser. Verhoeff Collection.

calcivagus Verhoeff (1908c : 140, 144)

SYNTYPES : two males. Reg. no. 1908:6:1:31-32. Lake Como, Italy. Verhoeff Collection.

SYNTYPE : female. Reg. no. 1921:6:10:81. Lake Como, Italy. Verhoeff Collection.

carynthiacus Verhoeff (1908c : 136) [Now *Androniscus roseus* (C. L. Koch)]

SYNTYPES : four females. Reg. no. 1908:6:1:26-29. Korinthia, Greece. Verhoeff Collection.

cavernarum Verhoeff (1908c : 136)

SYNTYPES : two males. Reg. no. 1908:6:1:24-25. Ukraine, USSR. Verhoeff Collection.

cavernarum strasseri Verhoeff (1928c : 157)

SYNTYPES : one male ; one female. Reg. no. 1928:7:4:79-80. Istrien, Italy. Verhoeff Collection.

dentiger Verhoeff (1908c : 139, 143)

SYNTYPES : one male ; one female. Reg. no. 1908:6:1:33-34. Italian Riviera. Verhoeff Collection.

dentiger ligulifer Verhoeff (1908c : 139)

SYNTYPE : male. Reg. no. 1908:6:1:35. Bologna, Italy. Verhoeff Collection.

roseus hamuligerus Verhoeff (1928c : 158)

SYNTYPES : two females. Reg. no. 1928:7:4:81-82. Ukraine, USSR. Verhoeff Collection.

subterraneus medius Verhoeff (1930b : 12)

SYNTYPES : one male ; one female. Reg. no. 1930:5:26:32-33. Friaul. Verhoeff Collection.

subterraneus noduliger Verhoeff (1929b : 30)

SYNTYPES : two males. Reg. no. 1930:5:26:30-31. Friaul. Verhoeff Collection.

subterraneus scaber Verhoeff (1930b : 13)

SYNTYPE (?) : male. Reg. no. 1930:5:26:34. Friaul. Collected by K. Strasser. Verhoeff Collection.

SYNTYPE : micropreparation. Reg. no. 1931:4:27:98. Villanova, Italy. Verhoeff Collection.

BURESCHIA Verhoeff*bulgarica* Verhoeff (1926b : 140)

SYNTYPE : male. Reg. no. 1928:7:4:78. Bulgaria. Collected by Buresch. Verhoeff Collection.

CHAVESIA Dollfus

costulata Dollfus (1889 : 2) [Now *Haplophthalmus danicus* Budde-Lund]

SYNTYPES : two females. Reg. no. 1911:11:8:10553. Açores Is. January 1889. Collected by Lt Chaves. A. M. Norman Collection (ex Dollfus Collection).

CYPHONISCELLUS Verhoeff

gottscheensis Verhoeff (1927a : 204)

SYNTYPES : five males ; one female. Reg. no. 1928:7:4:56-60. Krain. Verhoeff Collection.

styricus Verhoeff (1930b : 14)

SYNTYPES : two males. Reg. no. 1930:5:26:39-40. Styria. Verhoeff Collection.

HAPLOPHTHALMUS Schöbl

abbreviatus Verhoeff (1928c : 155)

SYNTYPES : two males. Reg. no. 1928:7:4:113-114. Ukraine, USSR. Verhoeff Collection.

apuanus Verhoeff (1908b : 190, 193)

SYNTYPES : two females. Reg. no. 1908:6:1:5. Italian Riviera. Verhoeff Collection

danicus Budde-Lund (1885 : 250)

SYNTYPES : c. 100 specimens, males, females and juveniles. Reg. no. 1921:10:18:311-322. Haunia. Budde-Lund Collection.

fumaranus Verhoeff (1908b : 189, 190)

SYNTYPE : female. Reg. no. 1908:6:1:2. Fiume, Italy. Verhoeff Collection.

fumaranus dolinensis Verhoeff (1908b : 189, 192)

SYNTYPES : one male, one female. Reg. no. 1908:6:1:3-4. Dolina, Ukraine, USSR. Verhoeff Collection.

siculus Dollfus (1896b : 5)

SYNTYPES : one male, one female. Reg. no. 1911:11:8:10840-41. Lake Lentini, Sicily, 'damp earth near lake'. Collected by A. Dollfus. A. M. Norman Collection (ex Dollfus Collection).

SYNTYPES : two females. Reg. no. 1921:10:18:393-395. Lake Lentini, Sicily. Collected by A. Dollfus. Budde-Lund Collection (ex Dollfus Collection).

HYLONISCUS Verhoeff

adonis Verhoeff (1927a : 219, 222)

SYNTYPES : three males ; two juveniles. Reg. no. 1928:7:4:71-75. Krain. Verhoeff Collection.

crassicornis Verhoeff (1926b : 155)

SYNTYPE : female. Reg. no. 1928:7:4:77. Bulgaria. Verhoeff Collection.

dalmaticus Verhoeff (1930b : 7)

SYNTYPES : one male ; one female. Reg. no. 1930:5:26:37-38. Dalmatia, Yugoslavia. Verhoeff Collection.

inflatus Verhoeff (1927a : 218, 221)

SYNTYPE : male. Reg. no. 1908:6:1:42. Siebenbergen. Verhoeff Collection.

mariae Verhoeff (1908a : 376)

SYNTYPE : male. Reg. no. 1908:6:1:40. Tatra. Verhoeff Collection.

narentanus Verhoeff (1908a : 375) [Nom. nov. for *Trichoniscus vividus* Verhoeff from Hercegovini]

SYNTYPES : four females. Reg. no. 1908:6:1:36-39. Hercegovini, Yugoslavia. Verhoeff Collection.

SYNTYPES : one male ; one female. Reg. no. 1921:6:10:82-83. Hercegovini, Yugoslavia. Verhoeff Collection.

refugiorum Verhoeff (1933 : 41)

SYNTYPES : two males ; three females. Reg. no. 1937:7:6:124-128. Apennine Mts, Europe. Verhoeff Collection.

IBERONISCUS Vandel

breuili Vandel (1952 : 351)

SYNTYPES : nine males ; fifteen females ; four juveniles. Reg. no. 1951:3:30:7-26. Old St Michael's Cave, Gibraltar. 6.3.1951 ; 'rotten wood ; 650 ft from entry'. Collected by T. R. Shaw. Presented by the Cave Research Group of Great Britain.

MIKTONISCUS Kesselyak

halophilus Blake (1931 : 345)

SYNTYPE : male (?) Reg. no. 1931:4:27:69. Massachusetts, USA. Verhoeff Collection.

NESIOTONISCUS Racovitza

corsicus corsicus (Racovitza) (1907 : 360) [*Trichoniscus* (*Nesiotoniscus*) *corsicus*]

SYNTYPES : one male ; one female. Reg. no. 1910:1:10:12-13. Grotte de Pietrabello, Corse, France. 9.1.1907. Presented by E. G. Racovitza.

ORITONISCUS Racovitza

flavus (Budde-Lund) (1906 : 83) [*Trichoniscus flavus*] [Nom. nov. for *Trichoniscus vividus* Budde-Lund (1885 : 246) nec. C. L. Koch]

SYNTYPES : one male ; five females. Reg. no. 1921:10:18:574-579. La Preste, France. Budde-Lund Collection.

pyrenaicus Racovitza (1907 : 193)

SYNTYPES : one male ; two females. Reg. no. 1910:1:10:6-8. Grotte d'Arudy, Arudy, dép. Basses-Pyrénées, France. 6.9.1905. Collected and presented by E. G. Racovitza.

PHYMATONISCUS Racovitza

tuberculatus (Racovitza) (1907 : 174) [*Trichoniscoides tuberculatus*]

SYNTYPES : three females. Reg. no. 1910:1:10:9-11. Grotte de l'Herm, Herm, Ariège, France. 30.9.1905. Collected and presented by E. G. Racovitza.

STYLOHYLEA Verhoeff

fagorum (Verhoeff) (1930b : 5) [*Trichoniscus* (*Stylohylea*) *fagorum*]

SYNTYPE : male. Reg. no. 1930:5:26:36. Croatia. Verhoeff Collection.

SYNTYPE : male. Reg. no. 1970:4:1. Croatia. Larwood Collection (ex Verhoeff Collection).

TITANETHES Schiödte**albus** (C. L. Koch) (1841 : 24) [*Pherusa alba*]

SYNTYPE : male. Reg. no. 1925:7:22:139. Adelsberg, Krain. Collected by K. Schmidt. Koch Collection.

dahli Verhoeff (1926b : 137) [Nom. nov. for *Titanethes albus* Verhoeff (1900 : 118)]

SYNTYPES : five females. Reg. no. 1928:7:4:83-87. Krain. Verhoeff Collection.

Subgenus **CYPHONETES** Verhoeff**hercegowinensis** Verhoeff (1900 : 118)

SYNTYPES : three males ; four juveniles. Reg. no. 1901:9:19:97-103. Hercegovini, Yugoslavia. Verhoeff Collection.

SYNTYPE : male. Reg. no. 1921:10:18:470. Hercegovini, Yugoslavia. Budde-Lund Collection (ex Verhoeff Collection).

TRICHONISCOIDES Sars**mixtus** (Racovitza) (1908 : 321) [*Trichoniscus (Trichoniscoides) mixtus*]

SYNTYPES : one male ; one female. Reg. no. 1910:1:10:1-2. Grotte de Baume-les-Messieurs, Jura, France. Presented by E. G. Racovitza.

modestus (Racovitza) (1908 : 306) [*Trichoniscus (Trichoniscoides) modestus*]

SYNTYPES : one male ; two females. Reg. no. 1910:1:10:3-5. Grotte de Rieufourcaud, Ariège, France. Presented by E. G. Racovitza.

scoparum Verhoeff (1908b : 176) [Now *Oritoniscus flavus* (Budde-Lund)]

SYNTYPE : female. Reg. no. 1908:6:1:12. Pyrenees (St Beat). Collected by H. Ribaut. Verhoeff Collection.

SYNTYPE : male. Reg. no. 1921:6:10:77. Pyrenees. Verhoeff Collection.

TRICHONISCUS Brandt**austriacus** Verhoeff (1908a : 376)

SYNTYPES : two males. Reg. no. 1921:6:10:79-80. S.E. Alps. Verhoeff Collection.

bosniensis Verhoeff (1901b : 75)

SYNTYPE : male. Reg. no. 1901:9:10:106-107. Bosna i Hercegovini, Yugoslavia. Verhoeff Collection.

cavernicola Budde-Lund (1885 : 246) [Now *Spelaeonethes medius* (Carl)]

SYNTYPES : three males ; five females. Reg. no. 1921:10:18:580-587. Pyrenees, 'in caves'. Budde-Lund Collection (ex Simon Collection).

commensalis Chilton (1901 : 191)

SYNTYPES : five males ; four females. Reg. no. 1952:4:18:1-9. Rai Valley, New Zealand. 1902 ; 'in nests of ants'. Collected by J. McMahon. Presented by G. Jackson.

elbanus Verhoeff (1931a : 564)

SYNTYPE : female. Reg. no. 1931:4:27:31. Elba I., Italy. Verhoeff Collection.

fragilis rharelbazi Racovitza (1908 : 289)

SYNTYPES : three males ; one female. Reg. no. 1910:1:10:14-17. Rharr-el-Baz, Algeria. Presented by E. G. Racovitza.

montanus Carl (1908 : 143) [*Trichoniscus vividus* var. *montanus*] [Now *Hyloniscus riparius* C. L. Koch]

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:438-439. St Gallen, Switzerland. Budde-Lund Collection (ex J. Carl Collection).

muscivagus Verhoeff (1917 : 52)

SYNTYPES : three females. Reg. no. 1931:4:27:13-16. Salzburg, Austria. Verhoeff Collection.

nivatus Verhoeff (1917 : 52)

SYNTYPES : two males ; one female. Reg. no. 1931:4:27:21-23. Salzburg, Austria. Verhoeff Collection.

noricus insulanus Verhoeff (1931a : 564)

SYNTYPES : two females. Reg. no. 1931:4:27:19-20. Elba I., Italy. Verhoeff Collection.

noricus sassanus Verhoeff (1931a : 565) [Now *Trichoniscus foveolatus* Vandel]

SYNTYPE : male. Reg. no. 1931:4:27:18. Lake Maggiore, Italy. Verhoeff Collection.

noricus sturanus Verhoeff (1931a : 565) [*Trichoniscus pusillus provisorius* Racovitza]

SYNTYPE : female. Reg. no. 1931:4:27:17. Piemonte. Verhoeff Collection.

SYNTYPES : three females. Reg. no. 1937:7:6:51-53. Piemonte. Verhoeff Collection.

pygmaeus Sars (1899 : 162)

SYNTYPE : micropreparation. Reg. no. 1911:11:8:564. Christiana, Norway. Norman Collection (ex G. O. Sars Collection).

SYNTYPES (?) : three females. Reg. no. 1911:11:8:10964-73. Norway. Norman Collection (ex G. O. Sars Collection).

stammeri Verhoeff (1932 : 21)

SYNTYPE : female. Reg. no. 1930:5:26:58. Krain. Verhoeff Collection.

verhoeffi Dahl (1919 : 209) [Now *Trichoniscus pusillus* Brandt]

SYNTYPES : one male ; four females. Reg. no. 1931:4:27:24-28. Bergamask Alps. Verhoeff Collection.

zosteræ Verhoeff (1931a : 563)

SYNTYPES : two females. Reg. no. 1931:4:27:29-30. Elba I., Italy. Verhoeff Collection.

SYNTYPE : fragments only. Reg. no. 1970:5:1. Elba I., Italy. Larwood Collection (ex Verhoeff Collection).

Family **BUDELUNDIELLIDAE****BUDELUNDIELLA** Silvestri***cateractæ*** Verhoeff (1930b : 30)

SYNTYPE : one specimen. Reg. no. 1930:5:26:41. Dalmatia, Yugoslavia. Verhoeff Collection.

Family **LIGIIDAE****EURLYLIGIA** Verhoeff***latissima*** Verhoeff (1926a : 349)

SYNTYPES : one male ; one female. Reg. no. 1928:7:4:21-22. Canala Berg, New Caledonia. Verhoeff Collection.

LIGIA Fabricius***cinerascens*** Budde-Lund (1885 : 265)

SYNTYPES : four males ; one female. Reg. no. 1921:10:18:1-5. Japan. Budde-Lund Collection.

dentipes Budde-Lund (1885 : 268)

SYNTYPE: female. Reg. no. 1921:10:18:12. Pulo Milu, Nicobar Is., Bay of Bengal. Budde-Lund Collection.

gracilipes Budde-Lund (1885 : 270)

SYNTYPES: one male; two females; one specimen in fragments. Landana, Angola, S.W. Africa. Budde-Lund Collection (ex Simon Collection).

melanocephala C. L. Koch (1838 : 18) [Now *Ligidium hypnorum* (Cuvier)]

SYNTYPES: six males; one female. Reg. no. 1925:7:22:104-110. Sugenheim, Bavaria, W. Germany. Koch Collection.

natalensis Collinge (1920 : 474)

PARATYPES: two males; eight females. Reg. no. 1919:4:26:371-380. Umhlali, Natal, May 1916, and Winkle Spruit Beach, South Coast, Natal, December 1916. Collected by C. Akerman. Presented by W. E. Collinge.

perkinsi (Dollfus) (1900 : 525) [*Geoligia perkinsi*]

SYNTYPES: three females. Reg. no. 1904:11:5:33-37 (part). Olaa, Hawaii. September 1896. 2000 ft. Collected by Perkins. Presented by the Joint Committee of the Royal Society and British Association for Investigating the Fauna of the Sandwich Is. per Dr David Sharp.

SYNTYPES: one male; one female. Reg. no. 1904:11:5:33-37 (part). Waimea Mts, Kauai I., Hawaiian Is. June 1894. 4000 ft. Collected by Perkins. Presented by the Joint Committee of the Royal Society and British Association for Investigating the Fauna of the Sandwich Is. per Dr David Sharp.

pigmentata Jackson (1922 : 699)

SYNTYPES: one male (?); one female. Reg. no. 1921:10:18:131. Suez. Budde-Lund Collection.

Subgenus **POGONOLIGIA** Jackson***muscorum*** Jackson (1927 : 130) [Now *Ligia (Pogonoligia) platycephala* (Van Name)]

HOLOTYPE: male. Reg. no. 1927:4:4:1. Matacas Waterfall, Trinidad, West Indies. 14.2.1926; 'in moss under waterfall'. Collected and presented by C. L. Withycombe.

PARATYPES: one male; six females. Reg. no. 1927:4:4:2-6. Matacas Waterfall, Trinidad, West Indies. 14.2.1926; 'in moss under waterfall'. Collected and presented by C. L. Withycombe.

LIGIDIUM Brandt***cursorium*** Budde-Lund (1885 : 256) [Now *Ligidium hypnorum* (Cuvier)]

SYNTYPES: four females. Reg. no. 1921:10:18:137-140. Zagreb, Yugoslavia. Budde-Lund Collection (ex Brusina Collection).

herzegowinense Verhoeff (1901a : 41)

SYNTYPES: two females. Reg. no. 1901:9:19:39-40. Zenica, Yugoslavia. Verhoeff Collection.

latum Jackson (1923 : 834)

SYNTYPES: five females. Reg. no. 1921:10:18:168-174. San Francisco, USA. Collected by G. Eisen. Budde-Lund Collection.

Subgenus **NIPPOLIGIDIUM** Borutsky***japonicum*** Verhoeff (1918 : 119)

SYNTYPES: four females. Reg. no. 1938:7:7:69-72. Japan. Verhoeff Collection.

Family STENONISCIDAE

PARASTENONISCUS Verhoeff

elbanus Verhoeff (1931a : 558) [Now *Stenoniscus pleonalis* Aubert & Dollfus]

SYNTYPES : one male ; two females. Reg. no. 1931:4:27:49-51. Elba I., Italy. Verhoeff Collection.

Family TENDOSPHAERIDAE

TENDOSPHAERA Verhoeff

brembana Verhoeff (1931b : 36)

SYNTYPES : two specimens. Reg. no. 1931:4:27:63-64. Alpi Bergamasche, Italy. Verhoeff Collection.

verrucosa Verhoeff (1930a : 166)

SYNTYPE : one specimen. Reg. no. 1930:5:26:75. Limone, Italy ('Seealpen'). Verhoeff Collection.

Family RHYSCOTIDAE

RHYSCOTOIDES Arcangeli

cubensis (Budde-Lund) (1908 : 300) [*Rhyscotus cubensis*]

HOLOTYPE (?) : fragment only. Reg. no. 1921:10:18:1023. Cuba. Budde-Lund Collection.

linearis (Budde-Lund) (1908 : 300) [*Rhyscotus linearis*]

HOLOTYPE : few fragments only. Reg. no. 1921:10:18:1025. Moheli I., Comores Archipelago, Indian Ocean. Collected by Voeltzkow. Budde-Lund Collection.

ortonedae (Budde-Lund) (1908 : 299) [*Rhyscotus ortonedae*]

SYNTYPES : eight males and two badly damaged specimens. Reg. no. 1921:10:18:1027-1038. Naranjito, Guayas, Ecuador. January 1901. Collected by V. Ortoneda. Budde-Lund Collection.

parallelus (Budde-Lund) (1893 : 119) [*Rhyscotus parallelus*]

SYNTYPES : ten males. Reg. no. 1921:10:18:1039-1049. Calvari Hill, Caracas, Venezuela. 20.7.1891. Collected by Meinert. Budde-Lund Collection.

SYNTYPES : three males. Reg. no. 1956:10:10:164-165. Calvari Hill, Caracas, Venezuela. 20.7.1891. Collected by F. Meinert. Presented by University College, Dundee.

RHYSCOTUS Budde-Lund

bicolor Barnard (1924 : 235)

SYNTYPES : thirty-six males ; five females. Reg. no. 1933:1:25:250-256. Ovamboland, S.W. Africa. Barnard Collection.

globiceps Budde-Lund (1908 : 301)

HOLOTYPE : few fragments only. Reg. no. 1921:10:18:1024. Loango, Congo. 6.7.1892. Collected by H. Brauns. Budde-Lund Collection.

nasatus Budde-Lund (1908 : 301)

HOLOTYPE : male. Reg. no. 1921:10:18:1026. Realejo, Nicaragua. 18.1.1903. Collected by C. F. Baker. Budde-Lund Collection.

sphaerocephalus Budde-Lund (1893 : 120)

SYNTYPES : two males. Reg. no. 1921:10:18:1050-1051. Caracas, Venezuela. 1891. Collected by Meinert. Budde-Lund Collection.

Family **SQUAMIFERIDAE****NIAMBIA** Budde-Lund**angusta** Budde-Lund (1909 : 63)

SYNTYPES : three males ; eight females. Reg. no. 1921:10:18:1408-1417. Steinkopf, Cape Province, S. Africa. August 1904. Budde-Lund Collection.

brunnea Budde-Lund (1909 : 61) [Now *Niambia truncata* (Brandt)]

SYNTYPES : six males ; twenty females. Reg. no. 1921:10:18:1418-1429. Kamaggas, Cape Province, S. Africa. July 1904. Collected by L. Schultze. Budde-Lund Collection.

flavescens Barnard (1924 : 233)

SYNTYPES : fifteen males ; twenty-eight females. Reg. no. 1933:1:25:140-149. Ondongwa, Ovamboland, S.W. Africa. Collected by K. H. Barnard and R. F. Lawrence. Presented by K. H. Barnard.

formicarum Barnard (1932 : 268)

SYNTYPES : eight males ; eight females. Reg. no. 1933:1:25:173-180. Matjiesfontein, Cape Province, S. Africa. Collected by W. F. Purcell. Barnard Collection.

griseoflavus Barnard (1924 : 234)

SYNTYPES : nine males ; five females. Reg. no. 1933:1:25:150-153. Andoni, Ovamboland, S.W. Africa. 1923. Collected and presented by K. H. Barnard.

hirsuta Budde-Lund (1909 : 62) [Now *Niambia truncata* (Brandt)]

HOLOTYPE (?) : male. Reg. no. 1921:10:18:1434. Port Elizabeth, S. Africa. 15.12.1898. Collected by Dr Brauns. Budde-Lund Collection (ex Hamburg Museum).

longicauda Barnard (1924 : 235)

SYNTYPES : thirteen males ; thirty-four females. Reg. no. 1933:1:25:181-190. Andoni, Ovamboland, S.W. Africa. 1923. Collected and presented by K. H. Barnard.

marginepapillosa Budde-Lund (1909 : 64) [Now *Niambia capensis* (Dollfus)]

HOLOTYPE : fragments only. Reg. no. 1921:10:18:1435. Simonstown, Cape Province, S. Africa. Budde-Lund Collection.

modesta Budde-Lund (1909 : 62)

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:1436-1438. Grootfontein, S.W. Africa. 10.1.1905. Collected by L. Schultze. Budde-Lund Collection.

pallida Budde-Lund (1909 : 61)

SYNTYPES : sixteen males ; thirteen females. Reg. no. 1921:10:18:1439-1450. Possession I. May 1903. Collected by Schultze. Budde-Lund Collection.

palmetensis Vandel (1959 : 517)

SYNTYPES : one male ; one female. Reg. no. 1973:473:2. Keta, Ghana. April 1958, 'diseased crown of coconut palm'. Presented by the Commonwealth Institute of Entomology (coll. no. 16732) (ex Ministry of Food and Agriculture, Kumasi, Ghana).

pusilla Budde-Lund (1909 : 63) [Now *Niambia capensis* (Dollfus)]

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:1451-1452. Simonstown, Cape Province, S. Africa. Budde-Lund Collection.

squamata (Budde-Lund) (1885 : 196) [*Leptotrichus squamatus*]

SYNTYPE : male. Reg. no. 1921:10:18:1453. Landana, Congo. Budde-Lund Collection.

Subgenus **MANIBIA** Barnard**lata** Barnard (1932 : 270)

HOLOTYPE : female. Reg. no. 1933:1:25:191. Sanyati Valley, S. Rhodesia. Collected by R. H. Stevenson. Barnard Collection.

microps Barnard (1932 : 271)

SYNTYPES : four females. Reg. no. 1933:1:25:192-194. Maxixe, Moçambique. Collected by R. F. Lawrence. Barnard Collection.

PLATYARTHUS Brandt**caudatus** Aubert & Dollfus (1890 : 10)

SYNTYPES : one male ; one female. Reg. no. 1911:11:8:10835-6. Marseille, France. Norman Collection (ex Dollfus Collection).

SYNTYPE : female. Reg. no. 1921:10:18:1549. Marseille, France. Budde-Lund Collection (ex Aubert Collection).

caudatus squamatus Verhoeff (1908b : 180) [Now *Platyarthrus caudatus* Aubert & Dollfus]

SYNTYPES : two females. Reg. no. 1908:6:1:22-23. Noli, Italian Riviera. Verhoeff Collection.

costulatus Verhoeff (1908b : 179)

SYNTYPES : one male ; two females. Reg. no. 1908:6:1:19-21. Italian Riviera. Verhoeff Collection.

schöbli Budde-Lund (1885 : 200)

SYNTYPES : three females. Reg. no. 1911:11:8:10837-39. Bona, Algeria. Collected by Meinert. Norman Collection.

SYNTYPES : two females. Reg. no. 1956:10:10:155. Bona, Algeria. Collected by Meinert. Presented by University College, Dundee.

TRICHORHINA Budde-Lund**micros** Budde-Lund (1913b : 383)

HOLOTYPE : fragment only. Reg. no. 1921:10:18:1607. Mauritius, Indian Ocean. Budde-Lund Collection.

minutissima Budde-Lund (1913b : 383)

SYNTYPES : one male ; two females. Reg. no. 1913:1:8:123-125. Siren I., Cargados Carajos, Indian Ocean. Collected by the 'Sealark' Expedition. Presented by J. S. Gardiner.

SYNTYPES : two males ; four females. Reg. no. 1921:10:18:1608-1612. Siren I., Cargados Carajos, Indian Ocean. Collected by the 'Sealark' Expedition. Budde-Lund Collection.

papillosa (Budde-Lund) (1893 : 123) [*Alloniscus papillosus*]

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:2163-2164. Caracas. Budde-Lund Collection.

Family **ONISCIDAE****ALLONISCUS** Dana**brevis** Budde-Lund (1885 : 226)

SYNTYPE : male. Reg. no. 1921:10:18:2113. 'Indes'. Collected by J. Ray. Budde-Lund Collection.

compar Budde-Lund (1893 : 124)

SYNTYPES : one male ; two females ; one other specimen in fragments. Reg. no. 1921:10:18:2137-2139. Caracas. Collected by Meinert. Budde-Lund Collection.

cornutus Budde-Lund (1885 : 228)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:2140-2141. California, USA. Budde-Lund Collection.

nacreus Collinge (1922 : 108)

SYNTYPES : one male ; five females. Reg. no. 1922:11:10:1-5. Tamatave, east coast of Madagascar. Collected by Herscell and Chauvin. Presented by P. A. Methuen.

porcellioides (Budde-Lund) (1904 : 45) [*Arhina porcellioides*]

SYNTYPES : two males. Reg. no. 1921:10:18:971-972. No locality. Budde-Lund Collection.

ANCHIPHILOSCIA Stebbing**cunningtoni** Stebbing (1908 : 557)

SYNTYPES : five males ; fifteen females. Reg. no. 1909:5:1:9-13. Niamkolo Bay, Lake Tanganyika, 'under stones'. Collected by W. A. Cunnington. Presented by the Tanganyika Exploration Committee.

SYNTYPE : one micropreparation. Reg. no. 1909:5:1:14. Niamkolo Bay, Lake Tanganyika ; 'under stones'. Collected by W. A. Cunnington. Presented by the Tanganyika Exploration Committee.

karongae Stebbing (1908 : 556) [Now *Setaphora suarezia* Budde-Lund]

SYNTYPES : two males ; four females. Reg. no. 1909:5:1:15-19. Kambwe, nr Karonga, Tanzania. 27.6.1904 ; 'on damp decaying wood close to swamp'. Collected by W. A. Cunnington. Presented by the Tanganyika Exploration Committee.

SYNTYPES : six micropreparations. Reg. no. 1909:5:1:20-25. Kambwe, nr Karonga, Tanzania. 27.6.1904 ; 'on damp decaying wood close to swamp'. Presented by the Tanganyika Exploration Committee.

APHILOSCIA Budde-Lund**vilis** (Budde-Lund (1885 : 210) [*Philoscia vilis*])

HOLOTYPE : in fragments. Reg. no. 1921:10:18:2090. Cape of Good Hope. Collected by Drege. Budde-Lund Collection.

ARMADILLONISCUS Uljanin**dalmatinus** Verhoeff (1901a : 39) [Now *Armadilloniscus littoralis* Budde-Lund]

SYNTYPES : one male ; one female. Reg. no. 1970:82:2. Dalmatia, Yugoslavia. Larwood Collection (ex Verhoeff Collection).

littoralis Budde-Lund (1885 : 237)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:1057-1058. Venetias. Collected by Schaufuss. Budde-Lund Collection.

BATHYTROPA Budde-Lund**granulata** Aubert & Dollfus (1890 : 9)

SYNTYPE : female. Reg. no. 1911:11:8:10549. Marseille, France. Norman Collection (ex Dollfus Collection).

hispana Dollfus (1893 : 50) [Now *Haplophthalmus danicus* Budde-Lund]

SYNTYPE : female. Reg. no. 1911:11:8:10546. Valencia, Spain. Norman Collection (ex Dollfus Collection).

SYNTYPE : female. Reg. no. 1921:10:18:376. Valencia, Spain. Budde-Lund Collection (ex Dollfus Collection).

meinerti Budde-Lund (1885 : 197)

SYNTYPES : two males. Reg. no. 1911:11:8:10550-51. Bona, Algeria. Collected by Meinert. Norman Collection (ex 'Zool. Mus. Haun.').

SYNTYPES : two females ; one other specimen in fragments. Reg. no. 1921:10:18:1518-1521. Bona, Algeria. Collected by Meinert. Budde-Lund Collection.

meinerti costata Budde-Lund (1885 : 198) [*Bathytropa costata*]

SYNTYPES : two females ; one other damaged specimen. Reg. no. 1921:10:18:1512-1514. Mt Bona, Algeria. Collected by Meinert. Budde-Lund Collection.

thermophila Dollfus (1896a : 28) [Now *Trichorhina tomentosa* (Budde-Lund)]

SYNTYPES : two females. Reg. no. 1911:11:8:10547-48. Serres du Muséum, Paris. Norman Collection (ex Dollfus Collection).

BENTHANA Budde-Lund**pauper** (Jackson) (1926 : 194) [*Philoscia (Benthana) pauper*]

SYNTYPE: one male; two micropreparations. Reg. no. 1921:10:18:1688. Valparaiso, Chile. Budde-Lund Collection (ex Michaelson Collection, Mus. Hamburg).

villosa (Jackson) (1926 : 195) [*Philoscia (Benthana) villosa*]

HOLOTYPE: female; one micropreparation. Reg. no. 1921:10:18:1674. Matucana, Peru. Budde-Lund Collection.

BILAWRENCIA Vandel**albicincta** Vandel (1973 : 74)

SYNTYPES: nine males; nine females. Reg. no. 1970:414:18. Vulavu, Santa Isabel, Solomon Is. 7.10.1965; 'village rubbish'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; one female. Reg. no. 1970:415:1. Fulakora Pt, Raja, Santa Isabel, Solomon Is. 30.9.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; nine females. Reg. no. 1970:416:9. Cockatoo I., Santa Isabel, Solomon Is. 19-20.9.1965; 'shore litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: four males; five females. Reg. no. 1970:417:13 (part). Tatamba, Santa Isabel, Solomon Is. 4.10.1965; 'mangrove litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: male. Reg. no. 1970:417:13 (part). Raja, N.E. Tatamba, Santa Isabel, Solomon Is. 30.9.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; one female. Reg. 1970:417:13 (part). Tatamba, Santa Isabel, Solomon Is. 6.10.1965; 'native gardens'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two males; four females. Reg. no. 1970:418:6. Lilihinia I., Santa Isabel, Solomon Is. 21.10.1965; 'shore litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; four females. Reg. no. 1970:419:4. E. Central San Jorge, Santa Isabel, Solomon Is. 24.9.1965; 'forest litter'. Collected by J. Peake and P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: fifty specimens, males, females and juveniles. Reg. no. 1970:421:50. Lunga Beach, Guadalcanal, Solomon Is. 31.8.1965; 'lagoon debris'. Collected by P. N. Lawrence. Presented by the Royal Society.

isabella Vandel (1973 : 78)

SYNTYPES: one hundred and seven specimens, males, females and juveniles. Reg. no. 1970:420:107. Vulavu, Santa Isabel, Solomon Is. 7.10.1965; 'village rubbish'. Collected by P. N. Lawrence. Presented by the Royal Society.

BURMONISCUS Collinge**kempi** Collinge (1916 : 127)

PARATYPES: two males; one female. Reg. no. 1919:4:26:500-502. Maosmai Cave, Cherrapunji, Assam, India. October 1914. c. 4000 ft. Collected by S. W. Kemp. Presented by W. E. Collinge.

CALMANESIA Collinge**methueni** Collinge (1922 : 109)

SYNTYPES : one male ; three females. Reg. no. 1922:11:10:6-9. Forest of Folohoy, East Madagascar. 1911. Collected by Herschell and Chauvin. Presented by P. A. Methuen.

SYNTYPES : three females. Reg. no. 1922:11:10:10-12. Analmazotra, Eastern Forest, Madagascar. June 1911 ; 'under rotten logs'. Collected and presented by P. A. Methuen.

CALYCUONISCUS Collinge**bodkini** Collinge (1915 : 509)

SYNTYPES : twenty males ; fifteen females. Reg. no. 1919:4:26:520-539. Botanic Gardens, Georgetown, Guiana ; 'under bark of trees'. Presented by W. E. Collinge.

CHAETOPHILOSCIA Verhoeff**balssi** Verhoeff (1928c : 170)

SYNTYPE : female. Reg. no. 1928:7:4:45. Glasshouse in Munich, Germany. Verhoeff Collection.

cellaria (Dollfus) (1884 : ?) [*Philoscia cellaria*]

SYNTYPE : male. Reg. no. 1892:12:6:5. Caves de Beaune, France. Collected by André. Presented by J. D'Arcy Thompson.

SYNTYPES : three males ; two females. Reg. no. 1911:11:8:10762-66. Caves de Beaune, France. Collected by E. André. Norman Collection (ex Dollfus Collection).

SYNTYPES : two males ; two females. Reg. no. 1921:10:18:1739-1742. Caves de Beaune, France. Budde-Lund Collection (ex Paris Museum).

SYNTYPES : three males ; two females. Reg. no. 1928:12:1:3667-3670. Caves de Beaune, France. Stebbing Collection (ex Dollfus Collection).

SYNTYPES : three males. Reg. no. 1956:10:10:171-173. Caves de Beaune, France. Collected by E. André. Presented by University College, Dundee (ex Dollfus Collection).

dorsalis Verhoeff (1928c : 138)

SYNTYPE : male. Reg. no. 1928:7:4:43. Italian Riviera. Verhoeff Collection.

elongata (Dollfus) (1884 : ?) [*Philoscia elongata*]

SYNTYPES : three females. Reg. no. 1911:11:8:10750-52. St Maxine, France. Norman Collection (ex Dollfus Collection).

formosana Verhoeff (1928a : 221)

SYNTYPES : one male ; two females. Reg. no. 1928:7:4:4-6. Formosa (Taiwan). Verhoeff Collection.

hastata Verhoeff (1929a : 133)

SYNTYPE : female. Reg. no. 1928:7:4:44. Bulgaria. 12.9.1923. Collected by I. Buresch. Verhoeff Collection.

meeusei Holthuis (1946 : 124)

SYNTYPES : one male ; two females. Reg. no. 1947:4:14:1-3. Victoria Regia House, Royal Botanic Gardens, Kew, England. 15.4.1936 ; 'under stones'. Collected by A. D. J. Meeuse. Presented by the Natural History Museum, Leiden.

pallida Verhoeff (1928c : 141) [Now *Chaetophiloscia cellaria* (Dollfus)]

SYNTYPE : female. Reg. no. 1928:7:4:42. French Riviera. Verhoeff Collection.

DETO Guérin**armata** Budde-Lund (1906 : 84)

SYNTYPES : one male ; two females. Reg. no. 1921:10:18:1074-1076. St Paul I., Indian Ocean. 26.4.1903. Budde-Lund Collection.

marina (Chilton) (1885 : 464) [*Philougria marina*]

SYNTYPE : female. Reg. no. 1921:10:18:1085. Coogee Bay, nr Sydney, New South Wales. 30.12.1883; 'in rock pools'. Collected by C. Chilton. Budde-Lund Collection (ex Dundee Museum).

robusta Budde-Lund (1906 : 87)

SYNTYPE : fragments only. Reg. no. 1921:10:18:1086. Auckland I., Pacific Ocean. Budde-Lund Collection.

DIACARA Budde-Lund**elegans** (Dollfus) (1895 : 186) [*Alloniscus elegans*]

SYNTYPE : female. Reg. no. 1921:10:18:1673. Mtgne d'Ambre, Diego-Suarez, Madagascar. Collected by Ch. Alluaud. Budde-Lund Collection (ex Dollfus Collection).

DIDIMA Budde-Lund**humilis** Budde-Lund (1908 : 292)

HOLOTYPE : female. Reg. no. 1921:10:18:1888. Antananarivo, Madagascar. Collected by F. Sikora. Budde-Lund Collection.

FORMOSOSCIA Verhoeff**ocellata** Verhoeff (1928a : 219)

SYNTYPE : female. Reg. no. 1928:7:4:9. Formosa. Verhoeff Collection.

HALOPHILOSCIA Verhoeff**adriatica** Verhoeff (1908a : 358)

SYNTYPES : two females. Reg. no. 1921:6:10:70-71. Nr Gulf of Fiume (Rijeka), Yugoslavia. Verhoeff Collection.

adriatica rupium Verhoeff (1931a : 548) [Now *Halophiloscia couchi* (Kinahan)]

SYNTYPE : female. Reg. no. 1930:5:26:46. Noli, Italy. Verhoeff Collection.

fucorum Verhoeff (1930b : 36) [Now *Halophiloscia couchi* (Kinahan)]

SYNTYPE : female. Reg. no. 1930:5:26:45. Split, Yugoslavia. 1928. Verhoeff Collection.

gracilicornis Verhoeff (1939 : 218) [Now *Halophiloscia hirsuta* Verhoeff]

SYNTYPE : female. Reg. no. 1938:7:7:61. Apulia, Lecce (?), Italy. Verhoeff Collection.

hirsuta Verhoeff (1928c : 132)

SYNTYPE : female. Reg. no. 1931:4:27:12. St Maxime, Toscana, Italy. 25th April. Verhoeff Collection.

tyrrhena Verhoeff (1928c : 131)

SYNTYPES : four females; one juvenile. Reg. no. 1928:7:4:35-39. Riviera. Verhoeff Collection.

SYNTYPES : two males; three females. Reg. no. 1937:7:6:100-104. Riviera. Verhoeff Collection.

HANONISCUS Budde-Lund**tuberculatus** Budde-Lund (1912 : 42)

SYNTYPES : one male; three females. Reg. no. 1921:10:18:5735-5738. W. Australia. Budde-Lund Collection.

HIATONISCUS Barnard**contractus** Barnard (1932 : 285)

SYNTYPES : four males ; three females. Reg. no. 1933:1:25:246-249. Swellendam, Langeberg Mts, Cape Province. 1925. Collected and presented by K. H. Barnard.

griseus Barnard (1932 : 283)

SYNTYPES : twenty-nine males ; twenty-eight females and juveniles. Reg. no. 1933:1:25:234-245. Table Mt, Cape Province, S. Africa. Barnard Collection.

HORA Barnard**damae** Barnard (1932 : 230)

SYNTYPES : two males ; one female. Reg. no. 1933:1:25:60-62. Swellendam, Langeberg Range, Cape Province. 1925. 3500-4000 ft. Collected and presented by K. H. Barnard.

ISABELLOSCIA Vandel**heroldi** Vandel (1973 : 54)

SYNTYPES : four females ; five juveniles. Reg. no. 1970:427:9. Thousand Ships Bay, Lilihinia I., Santa Isabel, Solomon Is. 20.9.1965 ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : two males ; twelve females ; six juveniles. Reg. no. 1970:428:15. Tatamba, Santa Isabel, Solomon Is. 27.9.1965 ; 'litter under *Casuarina*'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : one male ; one female. Reg. no. 1970:429:2. Thousand Ships Bay, opposite Lilihinia I., S.E. Santa Isabel, Solomon Is. 20.9.1965 ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

ISCHIOSCIA Verhoeff**debilis** (Budde-Lund) (1893 : 121) [*Philoscia debilis*]

SYNTYPES : four females. Reg. no. 1921:10:18:2236-2239. La Moka. August 1891. Collected by F. Meinert. Budde-Lund Collection.

JAPANONISCUS Verhoeff**balsii** Verhoeff (1928b : 32)

SYNTYPE : female. Reg. no. 1928:7:4:1. Aburatsubo, nr Misaki, Japan. 13.10.1904. Collected by H. Sauter. Verhoeff Collection.

KRANTZIA Barnard**poecila** Barnard (1932 : 281)

SYNTYPES : one male ; three females. Reg. no. 1933:3:18:7-11. Krantz kop, Natal, S. Africa. 1917. Presented and collected by K. H. Barnard.

LABYRINTHASIUS Verhoeff**graecus** Verhoeff (1929c : 119) [Now *Bathytropa granulata* Aubert & Dollfus]

SYNTYPE : female. Reg. no. 1930:5:6:26. Crete. 7.1.1929. Verhoeff Collection.

LEPIDONISCUS Verhoeff*germanicus carniolense* Verhoeff (1928c : 127)

SYNTYPE : female. Reg. no. 1928:7:4:28. Krain. Verhoeff Collection.

pruinus denticulatus Verhoeff (1928c : 126)

SYNTYPES : two males ; four females. Reg. no. 1928:7:4:23-27. Italy. Verhoeff Collection.

MARIONISCUS Barnard*spatulifrons* Barnard (1932 : 234)

SYNTYPES : ten males ; twelve females. Reg. no. 1933:1:25:67-74. Hout Bay, Cape Peninsula, S. Africa. Collected and presented by K. H. Barnard.

NAHIA Budde-Lund*hirsuta* (Budde-Lund) (1906 : 89) [*Philoscia hirsuta*]

SYNTYPES : mixed with other (non-type) specimens collected by Schultze in Cape Town. Reg. no. 1921:10:18:2022-2033. Simonstown, S. Africa. 19.6.1903. Budde-Lund Collection.

OLIBRINUS Budde-Lund*pigmentatus* Budde-Lund (1913b : 390)

SYNTYPES : two females. Reg. no. 1913:1:8:154-155. Coin, Peros, Chagos Archipelago, Indian Ocean. Collected by the Percy Sladen Trust Expedition. Presented by J. S. Gardiner.

ONISCUS Linnaeus*kenepurensis* Chilton (1901 : 135)

SYNTYPES : four males. Reg. no. 1900:11:1:43-46. Kenepuru, New Zealand. Presented by C. Chilton.

simoni Budde-Lund (1885 : 205)

SYNTYPE : female. Reg. no. 1911:11:8:10650. St Jean de Luz, nr Bayonne, France. Collected by E. Simon. Norman Collection (ex Dollfus Collection).

SYNTYPE : female. Reg. no. 1921:10:18:5689. Lac Marescot, nr Biarritz, France. Collected by E. Simon. Budde-Lund Collection.

ORONISCUS Verhoeff*dolomiticus* Verhoeff (1908a : 347)

SYNTYPE : female. Reg. no. 1908:6:1:18. Tyrol, Austria. Verhoeff Collection.

SYNTYPE : female. Reg. no. 1921:6:10:39. Tyrol, Austria. Verhoeff Collection.

SYNTYPE : male (micropreparation). Reg. no. 1931:4:27:100. Ampezzo, Italy. Verhoeff Collection.

SYNTYPES : three females. Reg. no. 1937:7:6:121-123. Dolomite Mts. Verhoeff Collection.

PAPUAPHILOSCIA Vandel*bougainvillei* Vandel (1973 : 57)

SYNTYPE : one damaged specimen (abdomen missing). Reg. no. 1970:404:1. Popamansiu, Guadalcanal, Solomon Is. 1-4.11.1965. 4400 ft ; 'mossy ridge, forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

PAPUASONISCUS Vandel**holthuisi** Vandel (1973 : 25)

SYNTYPES: male; female. Reg. no. 1970:405:2. Raja, nr Fulakora Pt, Santa Isabel, Solomon Is. 30.9.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: male. Reg. no. 1970:406:1. Cockatoo I., Santa Isabel, Solomon Is. 19-20.9.1965; 'shore litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; seven females. Reg. no. 1970:407:7. Lilihinia I., Santa Isabel, Solomon Is. 21.9.1965; 'shore litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two males. Reg. no. 1970:408:16 (part). Tatamba, Santa Isabel, Solomon Is. 28-29.9.1965; 'coconut and *Casuarina* litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:408:16 (part). Tatamba, Santa Isabel, Solomon Is. 27.9.1965; 'litter under *Casuarina*'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:408:16 (part). Tatamba, Santa Isabel, Solomon Is. 4.10.1965; 'mangrove litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; one damaged female. Reg. no. 1970:408:16 (part). Tatamba, Santa Isabel, Solomon Is. 6.10.1965; 'native gardens'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two males; six females. Reg. no. 1970:408:16 (part). Raja, N.E. Tatamba, Santa Isabel, Solomon Is. 30.9.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two males; one female. Reg. no. 1970:409:3. Opposite Cockatoo I., S.E. Santa Isabel, Solomon Is. 19-20.9.1965; 'shore litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; one female. Reg. no. 1970:410:2. Umasami River, 5 mls S.W. Tamboko, Guadalcanal, Solomon Is. 7-10.7.1965; '*Areca* palm and litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:411:1. Mt Austern, nr Honiara, Guadalcanal, Solomon Is. 24.8.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: male. Reg. no. 1970:412:1. nr Mt Gallego, 6 mls S.W. Tamboko, Guadalcanal, Solomon Is. 4.7.1965; 'disturbed forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two males; one female. Reg. no. 1970:413:3. 7 mls S. of Wainoni, San Cristobal, Solomon Is. 2.7.1965; 'litter of palms, vines and ferns'. Collected by P. N. Lawrence. Presented by the Royal Society.

PARAPHILOSCIA Stebbing**armata** Vandel (1973 : 99)

SYNTYPES: two males; eleven females. Reg. no. 1970:386:13. Mt Austen, nr Honiara, Guadalcanal, Solomon Is. 24.8.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

lateralis (Budde-Lund) (1913b : 372) [*Pseudophiloscia lateralis*]

SYNTYPES: four females. Reg. no. 1913:1:8:35-40. Silhouette, Seychelle Is. Collected by the 'Sealark' Expedition. Presented by J. Stanley Gardiner.

SYNTYPES: two males; two females. Reg. no. 1913:1:8:41-44. Mt Sebert, Seychelle Is. 2.12.1905. 1800 ft. Collected by the 'Sealark' Expedition. Presented by J. Stanley Gardiner.

SYNTYPES : four females. Reg. no. 1913:1:8:45-47. Mt Alphonse, Cascade, Mahe I., Seychelle Is. 4.12.1905. 1800 ft. Collected by the 'Sealark' Expedition. Presented by J. Stanley Gardiner.

SYNTYPES : six males ; ten females. Reg. no. 1921:10:18:981-992. Palm, Mahe I., Seychelle Is. 2-8.5.1901. Collected by A. Brauer. Budde-Lund Collection.

mendanai Vandel (1973 : 93)

SYNTYPES : sixty specimens : males, females and juveniles. Reg. no. 1970:399:60. Nuhu, Guadalcanal, Solomon Is. 28-31.10.1965. 1000 ft ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : seven females. Reg. no. 1970:400:20 (part). 5 miles S.W. Tamboko, River Umasami, Guadalcanal, Solomon Is. 7.7.1965. 1000 ft ; 'ridge, forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : three males ; two females. Reg. no. 1970:400:20 (part). S.W. end of Monitor Creek, River Umasami, Guadalcanal, Solomon Is. 5.7.1965 ; 'forest litter in a hollow'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : three males ; three females. Reg. no. 1970:400:20 (part). nr Monitor Creek, Umasami River, Guadalcanal, Solomon Is. 5.7.1965 ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE : female. Reg. no. 1970:400:20 (part). Monitor Creek, River Umasami, Guadalcanal, Solomon Is. 5.7.1965 ; 'litter on mat of forest roots'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : two females. Reg. no. 1970:401:4. Mt Gallego, Guadalcanal, Solomon Is. 12.7.1965 ; 'ridge forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE : female. Reg. no. 1970:401:4 (part). Mt Gallego, Guadalcanal, Solomon Is. 12.7.1965. 3000 ft ; 'moss forest'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : two males ; three females. Reg. no. 1970:402:5. nr Mt Gallego, 6 mls S.W. Tamboko, Guadalcanal, Solomon Is. 4.7.1965 ; 'disturbed forest'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE : male. Reg. no. 1970:403:1. Tambeluse, Guadalcanal, Solomon Is. 1.11.1965. c. 1500 ft ; 'dry ridge litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

propinqua Vandel (1973 : 90)

SYNTYPES : thirty-six specimens : males, females and juveniles. Reg. no. 1970:390:36. nr Kuzi, Kolombangara, Solomon Is. 3-9.9.1965 ; 'forest litter' and 'coral limestone'. Collected by P. N. Lawrence and Isiah. Presented by the Royal Society.

SYNTYPES : thirty-five specimens : males, females and juveniles. Reg. no. 1974:59:35. nr Kuzi, Kolombangara, Solomon Is. 3-9.9.1965 ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

sancristobali Vandel (1973 : 100)

SYNTYPES : two males ; nine females ; four damaged adults. Reg. no. 1970:387:22 (part). Confluence of Warahito and Pagato Rivers, San Cristobal, Solomon Is. 23 and 29.7.1965 ; 'rotten wood and forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : one male ; three females. Reg. no. 1970:387:22 (part). 4 miles up Warahito from River Pagato, San Cristobal, Solomon Is. 4.8.1965 ; 'forest litter'. Collected by Leone and Isiah. Presented by the Royal Society.

SYNTYPES : one male ; three females. Reg. no. 1970:387:22 (part). Confluence of Warahito and Pagato Rivers, San Cristobal, Solomon Is. 1.8.1965 ; 'stream litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : two females. Reg. no. 1970:388:6 (part). c. 6.75 miles S. Wainoni, San Cristobal, Solomon Is. 24.7.1965 ; 'forest litter, ridge bottom'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: male. Reg. no. 1970:388:6 (part). S.E. Wainoni, San Cristobal, Solomon Is. 10.8.1965. 1650 ft; 'moss forest'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; two females. Reg. no. 1970:388:6 (part). nr Wainoni, San Cristobal, Solomon Is. 8.8.1965. 1000 ft; 'ridge litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: three males; four females. Reg. no. 1970:389:8. Huni River estuary, N.E. Wainoni, San Cristobal, Solomon Is. 9-12.8.1965; 'forest litter on coral limestone'. Collected by P. N. Lawrence. Presented by the Royal Society.

santaisabellae Vandel (1973:92)

SYNTYPES: three males; nine females. Reg. no. 1970:391:10. Thousand Ships Bay, opposite Lilihinia I., Santa Isabel, Solomon Is. 20.9.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: seventy-two specimens: males, females and juveniles. Reg. no. 1970:392:72. N.E. Tatamba, Raja, Santa Isabel, Solomon Is. 30.9.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: six males; thirteen females. Reg. no. 1970:393:8. Fulakora Pt, Raja, Solomon Is. 30.9.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; three females. Reg. no. 1970:394:4. Cockatoo I., Santa Isabel, Solomon Is. 19-20.9.1965; 'shore litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: four males; eight females. Reg. no. 1970:395:12. Lilihinia I., Santa Isabel, Solomon Is. 21.9.1965; 'shore litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:396:1. S.E. San Jorge, S. of Santa Isabel, Solomon Is. 22.9.1965; 'gully litter'. Collected by J. Peake and P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: three females. Reg. no. 1970:397:3. E. central San Jorge I., Santa Isabel, Solomon Is. 24.9.1965; 'forest litter'. Collected by J. Peake and P. N. Lawrence. Presented by the Royal Society.

PHALLONISCUS Budde-Lund

anomalus (Dollfus) (1890:4) [*Philoscia anomala*]

SYNTYPES: three males; two females. Reg. no. 1927:5:14:29-38 (part). Valparaiso, Chile. November 1875. 'Challenger' Collection.

SYNTYPES: six males; four females. Reg. no. 1927:5:14:29-38 (part). Juan Fernandez I., Pacific Ocean, 'beach'. 'Challenger' Collection.

pygmaeus (Budde-Lund) (1885:212) [*Philoscia pygmaea*]

SYNTYPES: two females (in fragments). Reg. no. 1921:10:18:1961-1962. Corsica. Collected by E. Simon. Budde-Lund Collection.

PHILOSCIA Latreille

affinis Verhoeff (1908a:352) [*Philoscia muscorum affinis*]

SYNTYPES: seven females. Reg. no. 1921:6:10:61-65. Southern Italy. Verhoeff Collection.

SYNTYPES: seven females. Reg. no. 1928:7:4:29-33. Italian Riviera. Verhoeff Collection.

SYNTYPE: female. Reg. no. 1931:4:27:72. Toscana region, Italy. Verhoeff Collection.

dalmatica Verhoeff (1901c:146) [*Philoscia muscorum dalmatica*]

SYNTYPES: two males. Reg. no. 1901:9:19:55-56. Dalmatia, Yugoslavia. Verhoeff Collection.

dilectum Collinge (1917 : 579) [Now *Aphiloscia vilis* (Budde-Lund)]

PARATYPES : seven males ; nine females. Reg. no. 1919:4:26:459-468. Pentrich, nr Pietermaritzburg, Natal, S. Africa. 14.9.1915. Collected by C. Akerman. Collinge Collection.

diminuta Budde-Lund (1893 : 120)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:1785-1786. La Moka, August 1891. Collected by F. Meinert. Budde-Lund Collection.

flava Budde-Lund (1913a : 70)

HOLOTYPE : female. Reg. no. 1921:10:18:1878. Victoria, Australia. Collected by Hauschild. Budde-Lund Collection.

gravosensis Verhoeff (1901c : 145)

SYNTYPE : female. Reg. no. 1901:9:19:54. Dalmatia, Yugoslavia. Verhoeff Collection.

guernei Dollfus (1887 : 195)

SYNTYPE : female. Reg. no. 1911:11:8:10772. Caldeira volcano, Faial I., Azores. 16.7.1887. Norman Collection.

longicornis Budde-Lund (1885 : 221) [Now *Halophiloscia couchi* (Kinahan)]

SYNTYPES : four males ; one female. Reg. no. 1921:10:18:2232-2235. Algiers. Collected by E. Simon. Budde-Lund Collection.

muscorum biellensis Verhoeff (1935 : 108)

SYNTYPES : one male ; two females. Reg. no. 1937:7:6:43-45. Piemonte region, Italy. Verhoeff Collection.

muscorum frigidana Verhoeff (1928c : 136)

SYNTYPE : female. Reg. no. 1928:7:4:34. Italian Riviera. Verhoeff Collection.

muscorum triangulifera Verhoeff (1918 : 157)

SYNTYPES : two females. Reg. no. 1921:6:10:68-69. Italian Riviera. Verhoeff Collection.

nitida (Miers) (1877 : 670) [*Philougria nitida*]

SYNTYPES : six females. Reg. no. 1879:21. Peru or Guiana. Presented by E. J. Miers (ex Wrzesniowsky Collection).

patienici Bagnall (1908 : 429)

SYNTYPES : five females. Reg. no. 1911:6:6:98-102. Botanical Gardens, Kew, Surrey, 'from West Indian plants'. Presented by R. S. Bagnall.

pulchella Budde-Lund (1885 : 214) [Now *Chaetophiloscia elongata* (Dollfus)]

SYNTYPES : three males. Reg. no. 1921:10:18:2017-2019. No locality. Budde-Lund Collection.

seriepunctata Budde-Lund (1893 : 122)

HOLOTYPE : female. Reg. no. 1921:10:18:1964. Caracas, Venezuela. 14.7.1891. Collected by Fr. Meinert. Budde-Lund Collection.

subterranea Budde-Lund (1912 : 40)

HOLOTYPE : few fragments only. Reg. no. 1921:10:18:1965. Yallingup, W. Australia. 5.10.1905. Budde-Lund Collection.

vittata Say (1818 : 429)

SYNTYPE : female (dry). Reg. no. 1973:511:1. United States. Presented by T. Say.

warreni Collinge (1917 : 578) [Now *Nahia hirsuta* (Budde-Lund)]

PARATYPES : three males ; nine females. Reg. no. 1919:4:26:469-478. Umbilo Bush, nr Durban, Natal, S. Africa. 16.9.1915. Collected by E. Warren. Collinge Collection.

Subgenus **BENTHANOPS** Barnard

fulva Barnard (1932 : 247)

SYNTYPES : eleven males ; thirty-nine females. Reg. no. 1933:1:25:118-129. Table Mt, Cape Peninsula, S. Africa. Barnard Collection.

Subgenus *KOMATIA* Barnard*marginata* Barnard (1932 : 240)

SYNTYPE : male. Reg. no. 1933:1:25:86. Wanetsi River, Portuguese East Africa. Collected by H. W. Bell-Marley. Barnard Collection.

PLYMOPHILOSCIA Warhberg*montana* Verhoeff (1926a : 335)

SYNTYPE : female. Reg. no. 1928:7:4:20. New Caledonia. Verhoeff Collection.

PSEUDOPHILOSCIA Budde-Lund*angustissima* Budde-Lund (1913a : 373)

SYNTYPES : one male ; one female. Reg. no. 1913:1:8:48-49. Mt Alphonse, Mahe I., Seychelle Is. 3.12.1905. Collected by the 'Sealark' Expedition. Presented by J. Stanley Gardiner.

SYNTYPES : one male ; three females. Reg. no. 1921:10:18:973-976. Palm, Seychelle Is. 2.5.1901. Collected by A. Brauer. Budde-Lund Collection.

brevicornis Budde-Lund (1913a : 374)

SYNTYPE : female. Reg. no. 1921:10:18:977. New Zealand. Budde-Lund Collection.

fragilis Budde-Lund (1904 : 43)

HOLOTYPE : few fragments only. Reg. no. 1921:10:18:978. Howick, New Zealand. Budde-Lund Collection.

inflexa Budde-Lund (1904 : 43)

SYNTYPES : one male ; one female. Reg. no. 1921:10:18:979-980. Corral, Chile. October 1894. Collected by Plate. Budde-Lund Collection.

RENNELLOSCIA Vandel*macrocephala* Vandel (1973 : 48)

SYNTYPES : five females ; two juveniles. Reg. no. 1970:385:8. N. of Kuzi, Kolombangara, Solomon Is. 6.10.1965. 500 ft ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

novabritannica Vandel (1973 : 32)

SYNTYPES : two females. Reg. no. 1970:362:2. Thousand Ships Bay, opposite Lilihinia I., Santa Isabel, Solomon Is. 20.9.1965 ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : two males ; fourteen females. Reg. no. 1970:363:16. Mt Austern, nr Honiara, Guadalcanal, Solomon Is. 24.7.1965 ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : two males ; four females ; one damaged adult. Reg. no. 1970:364:7. Nuhu, Guadalcanal, Solomon Is. 28.10.1965. 1000 ft ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : one female ; one juvenile. Reg. no. 1970:365:13 (part). Popamanisiu, Guadalcanal, Solomon Is. 1-4.11.1965. 4400 ft ; 'mossy ridge, forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES : three males ; four females ; three juveniles ; one damaged adult. Reg. no. 1970:365:13 (part). Popamanisiu, Guadalcanal, Solomon Is. 6-8.11.1965. 7000 ft ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE : female. Reg. no. 1970:366:24 (part). Umasami River, nr Monitor Creek, Guadalcanal, Solomon Is. 5.7.1965 ; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: six males; fourteen females; four juveniles; one damaged adult. Reg. no. 1970:366:24 (part). Umasami River, 5 miles S.W. Tamboko, Guadalcanal, Solomon Is. 7-10.7.1965; '*Areca* palm and litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two males; one female. Reg. no. 1970:367:3. nr Mt Gallego, 6 miles S.W. Tamboko, Solomon Is. 4.7.1965; 'disturbed forest'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:368:1. Lunga Beach, Guadalcanal, Solomon Is. 31.8.1965; 'dry grass litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two females; two juveniles. Reg. no. 1970:369:5 (part). Popamanisiu, Guadalcanal, Solomon Is. 8-9.11.1965. 5700 ft; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:369:5 (part). Popamanisiu, Guadalcanal, Solomon Is. 5.11.1965. 7000 ft; 'bog masses around trees'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: two females. Reg. no. 1970:370:3 (part). Hidden Valley, nr Mt Gallego, Guadalcanal, Solomon Is. 3.7.1965. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: male. Reg. no. 1970:370:3 (part). Summit of Mt Gallego, Guadalcanal, Solomon Is. 12.7.1965. 3600 ft; 'fern litter and forest mosses'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:371:1. Lunga Beach, Guadalcanal, Solomon Is. 31.8.1965; 'tidal debris'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:372:1. Nuhu, Guadalcanal, Solomon Is. 28-31.10.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; two juveniles. Reg. no. 1970:373:3. Umasami River, c. 6 miles S.W. Tamboko, Guadalcanal, Solomon Is. 1.7.1965; 'forest litter, sandy soil'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: twenty-five specimens: males, females and juveniles. Reg. no. 1970:374:25. 6-10 miles S. of Wainoni, San Cristobal, Solomon Is. July and August 1965. Collected by P. N. Lawrence and Isiah. Presented by the Royal Society.

SYNTYPES: five males; six females; six juveniles. Reg. no. 1970:375:18. Huni River Estuary, N.E. Wainoni, San Cristobal, Solomon Is. 9-12.8.1965; 'forest litter on coral limestone'. Collected by Isiah. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:376:1. Warahito-Pagato confluence, San Cristobal, Solomon Is. 1.8.1965. 330 ft; 'arboreal litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPE: female. Reg. no. 1970:377:29 (part). 4 miles up Warahito River, from Pagato River, San Cristobal, Solomon Is. 4.8.1965; 'forest litter'. Collected by Leone and Isiah. Presented by the Royal Society.

SYNTYPES: two males. Reg. no. 1970:377:29 (part). Warahito-Pagato confluence, San Cristobal, Solomon Is. 1.8.1965; 'stream litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: twenty-six specimens: males, females and juveniles. Reg. no. 1970:377:29 (part). Warahito-Pagato confluence, San Cristobal, Solomon Is. 23-29.7.1965; 'rotten wood and forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: thirty specimens: males, females and juveniles. Reg. no. 1970:378:30. Wainoni and environs, San Cristobal, Solomon Is. July and August, 1965. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: twenty specimens: males, females and juveniles. Reg. no. 1970:379:22. nr Kuzi, Kolombangara, Solomon Is. 8.9.1965. 50 ft; 'valley litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: three males; seven females. Reg. no. 1970:380:18. nr Kuzi, Kolombangara, Solomon Is. 6.9.1965. 250 and 500 ft; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: thirty-four specimens: males, females and juveniles. Reg. no. 1970:381:34. nr Kuzi, Kolombangara, Solomon Is. 3-9.9.1965; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: three males; nine females. Reg. no. 1970:383:9. Ngaliu Hill, Pawa, Ugi, Solomon Is. 20.7.1965; 'secondary forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: three males; twelve females. Reg. no. 1970:383:15. N. of Kiai, Kolombangara, Solomon Is. 6.9.1965. 1000 ft; 'forest litter'. Collected by P. N. Lawrence. Presented by the Royal Society.

SYNTYPES: one male; six females. Reg. no. 1970:60:7. N. of Kuzi, Kolombangara, Solomon Is. 4.9.1965. 1500 ft; 'litter mossy wood'. Collected by P. N. Lawrence. Presented by the Royal Society.

SCYPHAX Dana

intermedius Miers (1876: 227) [Now *Scyphax ornatus* (Dana)]

HOLOTYPE: female. Reg. no. 1973:476:1. New Zealand. Donor unknown.

SCYPHONISCUS Chilton

waitatensis Chilton (1901: 128)

SYNTYPE: male. Reg. no. 1900:11:1:51-52. Blueskin Bay, Otago, New Zealand. Presented by C. Chilton.

SYNTYPE: male. Reg. no. 1921:10:18:1067. Blueskin Bay, Otago, New Zealand. Budde-Lund Collection (ex Dundee Museum Collection).

SETAPHORA Budde-Lund

angusticauda (Budde-Lund) (1885: 216) [*Philoscia angusticauda*]

SYNTYPES: one male; three females. Reg. no. 1921:10:18:2247-2250. Borneo, Indonesia. Budde-Lund Collection.

cingulata (Barnard) (1932: 244) [*Philoscia (Setaphora) cingulata*]

SYNTYPES: one male; nine females. Reg. no. 1933:1:25:87-92. Port Shepstone, Natal, S. Africa. 1912. Collected and presented by K. H. Barnard.

coeca (Budde-Lund) (1895: 611) [*Philoscia coeca*]

SYNTYPE: fragments only. Reg. no. 1921:10:18:2251. Moulmein, Burma. January 1887. Collected by L. Fea. Budde-Lund Collection.

comta (Budde-Lund) (1895: 611) [*Philoscia comta*]

SYNTYPE: male. Reg. no. 1921:10:18:2252. Mt Carin, Asciuii Ghecu, 1300-1400 m. Collected by L. Fea. Budde-Lund Collection.

demarcata (Barnard) (1932: 244) [*Philoscia (Setaphora) demarcata*]

SYNTYPES: four males; three females. Reg. no. 1933:1:25:93-97. Pietermaritzburg, Natal, S. Africa. 1917. Collected and presented by K. H. Barnard.

fasciata (Jackson) (1933: 151) [*Philoscia (Setaphora ?) fasciata*]

SYNTYPES: one male; three females. Reg. no. 1933:12:20:3-6. Penau Ridge, Uahuka, Marquesas Is. 5.3.1931. 2000 ft; 'in moss'. Presented by H. G. Jackson.

SYNTYPES: two males; two females. Reg. no. 1952:4:18:109-111. Hanamiai Valley, Tahuata, Marquesas Is. Presented by H. G. Jackson.

lubricata (Budde-Lund) (1895 : 610) [*Philoscia lubricata*]

SYNTYPES : two females. Reg. no. 1921:10:18:2264-2265. Burma. Budde-Lund Collection.

mina (Budde-Lund) (1885 : 219) [*Philoscia mina*]

SYNTYPES : two males ; one female. Reg. no. 1921:10:18:1899-1901. Cape, S. Africa. Collected by Drege. Budde-Lund Collection.

ovata Budde-Lund (1913b : 386)

SYNTYPES : seven males ; eight females. Reg. no. 1921:10:18:2291-2303. Seychelles, Indian Ocean. May 1901. Collected by A. Brauer. Budde-Lund Collection.

pallidemaculata Budde-Lund (1913b : 387)

SYNTYPES : two males ; two females. Reg. no. 1913:1:8:132-136. Mt Alphonse, Cascade, Mahé I., Seychelles. 4.12.1905. 1800 ft. Collected by the 'Sealark' Expedition. Presented by J. S. Gardiner.

SYNTYPES : one male ; four females. Reg. no. 1913:1:8:137-140. Mahé I., Seychelles. 3.12.1905. Collected by the 'Sealark' Expedition. Presented by J. S. Gardiner.

SYNTYPES : ten males ; nine females. Reg. no. 1921:10:18:2304-2315. Palm, Seychelles, Indian Ocean. April 1901. Collected by A. Brauer. Budde-Lund Collection.

pilosa Budde-Lund (1913b : 388)

SYNTYPES : five males ; one female. Reg. no. 1913:1:8:144-149. Salomon Is., Chagos Archipelago, Indian Ocean. Collected by the 'Sealark' Expedition. Presented by J. S. Gardiner.

SYNTYPES : four males ; six females. Reg. no. 1921:10:18:2328-2337. Salomon Is., Chagos Archipelago, Indian Ocean. Collected by the 'Sealark' Expedition. Budde-Lund Collection.

rafflesi (Jackson) (1936 : 77) [*Philoscia (Setaphora) rafflesi*]

SYNTYPES : two males. Reg. no. 1938:5:23:9-10. nr River Yum, Plus Valley, Perak, Malaysia. 1933. Presented by the Raffles Museum.

suarezia (Dollfus) (1895 : 186) [*Philoscia suarezia*]

SYNTYPES : specimens mixed with others from Nossi-Be collected by Voeltzkow. Reg. no. 1921:10:18:2351-2358. Diego-Suarez, Madagascar. Budde-Lund Collection (ex Dollfus Collection).

truncatella (Budde-Lund) (1902 : 379) [*Philoscia truncatella*]

SYNTYPE : few fragments only. Reg. no. 1921:10:18:2383. Malay Peninsula. Collected by the 'Skeat' Expedition. Budde-Lund Collection.

STENOPHILOSCIA Verhoeff***dalmatica*** Verhoeff (1930b : 38)

SYNTYPE : female. Reg. no. 1920:5:26:44. Dalmatia, Yugoslavia. Verhoeff Collection.

SYNTYPE : micropreparation. Reg. no. 1931:4:27:106. Split, Dalmatia, Yugoslavia. Verhoeff Collection.

glarearum Verhoeff (1908a : 359)

SYNTYPES : two males ; one female. Reg. no. 1921:6:10:72-74. Sicily. Verhoeff Collection.

TIROLOSCIA Verhoeff***corsica*** (Dollfus) (1888 : 10) [*Philoscia corsica*]

SYNTYPES : three females. Reg. no. 1911:11:8:10767-10769. Gravone River, Vizzavona, Corsica. July 1881. Collected by E. Chevreux. Norman Collection (ex Dollfus Collection).

SYNTYPES : one male ; two females. Reg. no. 1921:10:18:1750-1752. Vizzavona, Corsica. Budde-Lund Collection (ex Dollfus Collection).

elbana Verhoeff (1931a : 542)

SYNTYPE : female. Reg. no. 1931:4:27:9. Elba I. Verhoeff Collection.

SYNTYPE : female (micropreparation). Reg. no. 1931:4:27:81. Populonia, Italy. Verhoeff Collection.

esterelana (Verhoeff) (1918 : 155) [*Philoscia* (*Paraphiloscia*) *esterelana*]

SYNTYPE : female. Reg. no. 1921:6:10:67. Esterel, France. Verhoeff Collection.

macchiaie Verhoeff (1931a : 543) [Now *Tiroloscia corsica* (Dollfus)]

SYNTYPE : female. Reg. no. 1931:4:27:10. Elba I. Verhoeff Collection.

pyrenaica (Dollfus) (1897 : 11) [*Philoscia pyrenaica*]

SYNTYPE : female. Reg. no. 1911:11:8:10770. Ahusquy, nr Mauleon, France. Collected by H. Broelemann. Norman Collection (ex Dollfus Collection).

squamuligera bargensis Verhoeff (1935 : 106)

SYNTYPES : four females. Reg. no. 1937:7:6:105-108. Apennine Mts, Italy. Verhoeff Collection.

squamuligera briani (Verhoeff) (1931a : 545) [*Philoscia* (*Tiroloscia*) *squamuligera briani*]

SYNTYPE : female. Reg. no. 1931:4:27:8. Piemonte region, Italy. Verhoeff Collection.

squamuligera tendana Verhoeff (1931a : 545) [Now *Tiroloscia exigua exigua* (Budde-Lund)]

SYNTYPE : female. Reg. no. 1931:4:27:7. Limone ('Seelapen'), Italy. Verhoeff Collection.

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APPENDIX I

The Collection also contains a large number of specimens labelled as types, mostly from the Budde-Lund Collection, for which no reference can be found in published literature. It seems possible that these are specimens with manuscript names which have been incorporated into personal collections but which have never been published. A list of this material comprising some 68 items is given below, and a list of the manuscript names has been deposited in the library of the British Museum (Natural History).

Family TYLIDAE

Tylos sp.

Two specimens. Reg. no. 1905:3:13:5-6. Arauco, Chile. Collected by C. S. Reed. Purchased from Rosenberg.

Fragment. Reg. no. 1921:10:18:646. Arauco, Chile. Budde-Lund Collection.

Family STYLONISCIDAE

Styloniscus sp.

Two specimens. Reg. no. 1921:10:18:408-409. Corral, Chile. October 1894. Collected by Dr Plate. Budde-Lund Collection.

Styloniscus sp.

Two specimens. Reg. no. 1921:10:18:420-421. Auckland, New Zealand. Budde-Lund Collection.

Family **TRICHONISCIDAE***Haplophthalmus* sp.

Two specimens. Reg. no. 1921:10:18:301-302. Lake Como, Italy. Budde-Lund Collection.

Haplophthalmus sp.

Two specimens. Reg. no. 1921:10:18:303-304. Anzio. 4.4.1897. Collected by F. Silvestri. Budde-Lund Collection.

Two specimens. Reg. no. 1921:10:18:305-306. Ain Draham. Collected by F. Silvestri. Budde-Lund Collection.

Haplophthalmus sp.

Four specimens. Reg. no. 1921:10:18:307-310. Klagenfurt, Austria. Collected by M. Latzel. Budde-Lund Collection.

Hyloniscus sp.

One specimen. Reg. no. 1928:7:4:76. Krain. Verhoeff Collection.

Nesiotoniscus sp.

Four specimens. Reg. no. 1921:10:18:434-437. Sardinia. Collected by Major Forsyth. Budde-Lund Collection.

Schiodtia sp.

Two specimens. Reg. no. 1921:10:18:445-446. Liguria, Italy. March 1896. Collected by R. Gestro. Budde-Lund Collection.

Trichoniscus sp.

One specimen. Reg. no. 1921:10:18:193-196. Kirschhorn Pt, Heikelberg, W. Germany. 21.7.1901. Collected and presented by G. Budde-Lund.

Trichoniscus sp.

One specimen. Reg. no. 1928:7:4:70. Bulgar. Verhoeff Collection.

Trichoniscus sp.

Three specimens. Reg. no. 1921:10:18:254-256. Gr. Bossea. August 1888. Collected by A. Vacca. Budde-Lund Collection.

Family **SQUAMIFERIDAE***Platyarthrus* sp.

Twelve specimens. Reg. no. 1921:10:18:1537-1548. Tunis. Collected by F. Silvestri. Budde-Lund Collection.

Platyarthrus sp.

Twelve specimens. Reg. no. 1921:10:18:1525-1536. Rome, Italy. Collected by F. Silvestri. Budde-Lund Collection.

Platyarthrus sp.

One specimen. Reg. no. 1921:10:18:1587. Tunis. Collected by F. Silvestri. Budde-Lund Collection.

Platyarthrus sp.

Two specimens. Reg. no. 1921:10:18:1603-1604. Mt Capraro (?). Budde-Lund Collection.
One specimen. Reg. no. 1921:10:18:1605. Boccadifalco. 17.2.1896. Collected by F. Silvestri. Budde-Lund Collection.

Family **ONISCIDAE***Alloniscus* sp.

'Details' (i.e. parts dissected) from one specimen. Reg. no. 1921:10:18:2112. No locality. Budde-Lund Collection.

Aphiloscia sp.

Four specimens. Reg. no. 1921:10:18:2069-2072. Madagascar. Budde-Lund Collection.

Aphiloscia sp.

Five specimens. Reg. no. 1921:10:18:2073-2077. Madagascar. Budde-Lund Collection.

Armadilloniscus sp.

Five specimens. Reg. no. 1921:10:18:1052-1056. Ban Lem Ngop, Thailand. Collected by Th. Mortensen. Budde-Lund Collection.

Armadilloniscus sp.

One specimen. Reg. no. 1921:10:18:1059. Brasilia, Brazil. Budde-Lund Collection.

Bathytropa sp.

Three specimens. Reg. no. 1921:10:18:1515-1517. Botanic Gardens, Hamburg. Budde-Lund Collection.

Chaetophiloscia sp.

Two specimens. Reg. no. 1921:10:18:2020-2021. Corral, Chile. Collected by R. Paessler. Budde-Lund Collection.

Chaetophiloscia sp.

Two specimens. Reg. no. 1930:5:26:42-43. Dalmatia, Yugoslavia. Verhoeff Collection.

Deto sp.

Seven specimens. Reg. no. 1921:10:18:1078-1084. Rottneest I., W. Australia. Budde-Lund Collection.

Detonella sp.

One specimen. Reg. no. 1938:7:7:46. Sachalin I., Japan. Verhoeff Collection.

Hanoniscus sp.

Two specimens. Reg. no. 1921:10:18:5729-5730. W. Australia. Budde-Lund Collection.

Hanoniscus sp.

Four specimens. Reg. no. 1921:10:18:5731-5734. W. Australia. Budde-Lund Collection.

Lepidoniscus sp.

One specimen. Reg. no. 1930:5:26:56. Piemonte. Verhoeff Collection.

Phalloniscus sp.

One specimen. Reg. no. 1921:10:18:2037. Stephens Isle, New Zealand. Collected by Schauinsland. Budde-Lund Collection.

Phalloniscus sp.

Two specimens. Reg. no. 1921:10:18:2038-2039. Marlborough, New Zealand. Budde-Lund Collection (ex Dundee Museum Collection).

Phalloniscus sp.

Two specimens. Reg. no. 1921:10:18:2040-2041. New Zealand. Collected by C. Chilton. Budde-Lund Collection.

Phalloniscus sp.

One specimen. Reg. no. 1921:10:18:2052. Auckland, New Zealand. Collected by H. Süter (Museum Hamburg). Budde-Lund Collection.

Phalloniscus sp.

Five specimens. Reg. no. 1921:10:18:2053-2057. Auckland, New Zealand. Budde-Lund Collection (ex Museum Hamburg Collection).

Philoscia sp.

Eight specimens. Reg. no. 1921:10:18:1730-1737. Botanical Gardens, Hamburg. Budde-Lund Collection.

Philoscia sp.

One specimen. Reg. no. 1921:10:18:1738. No locality. Budde-Lund Collection.

Philoscia sp.

Two specimens. Reg. no. 1921:10:18:1743-1744. Baboner. Collected by F. Silvestri. Budde-Lund Collection.

Philoscia sp.

Three specimens. Reg. no. 1921:10:18:1875-1877. Summit of Mt Roraima. 8600 ft. Budde-Lund Collection.

Philoscia sp.

One specimen. Reg. no. 1888:8. Iguarasso, Brazil. Budde-Lund Collection.

Philoscia sp.

Three specimens. Reg. no. 1921:10:18:1879-1881. Tonkin, Mauson Mts. 2000-3000 ft. Collected by H. Frunstorfer. Budde-Lund Collection.

Philoscia sp.

Six specimens. Reg. no. 1921:10:18:1882-1887. Cameroons. Collected by Y. Sjostedt. Budde-Lund Collection.

Philoscia sp.

One specimen. Reg. no. 1921:10:18:1889. Turkestan. Collected by Uljanin. Budde-Lund Collection.

Philoscia sp.

Two specimens. Reg. no. 1907:4:30:23-24. Trinidad, West Indies. 18.10.1906. Named by G. Budde-Lund. Presented by the Earl of Crawford.

Philoscia sp.

Four specimens. Reg. no. 1921:10:18:1890-1893. Japan. Collected by Hilgendorf. Budde-Lund Collection.

Philoscia sp.

Seven specimens. Reg. no. 1921:10:18:1950-1956. Naranjito Province, Guayas. 9.3.1901. Collected by V. Ortoneda. Budde-Lund Collection.

Philoscia sp.

One specimen. Reg. no. 1907:4:30:21. Hackgall, Sri Lanka. Named by G. Budde-Lund. Presented by Dr Willey.

Philoscia sp.

One specimen. Reg. no. 1905:3:31:3. Arauco, Chile. Presented by C. S. Reid. One specimen. Reg. no. 1921:10:18:1966. Arauco, Chile. Budde-Lund Collection.

Philoscia sp.

Eight specimens. Reg. no. 1921:10:18:1967-1974. Bileundi. August 1891. Collected by Sjostedt. Budde-Lund Collection.

Setaphora sp.

Eleven specimens. Reg. no. 1921:10:18:2253-2263. Buitenzorg. Collected by K. Kraepelin. Budde-Lund Collection.

Setaphora sp.

Twelve specimens. Reg. no. 1921:10:18:2266-2277. Formosa. Collected by Bartels. Budde-Lund Collection.

Setaphora sp.

One specimen. Reg. no. 1921:10:18:2278. Galnit. Collected by Bartels. Budde-Lund Collection.

Setaphora sp.

Eighteen specimens. Reg. no. 1921:10:18:2279-2290. Formosa. Budde-Lund Collection.

Setaphora sp.

Twelve specimens. Reg. no. 1921:10:18:2316-2327. Botanical Gardens, Kew, Surrey. Collected by Bagnall. Budde-Lund Collection.

Setaphora sp.

Twelve specimens. Reg. no. 1921:10:18:2339-2350. Formosa. Budde-Lund Collection.

Setaphora sp.

One specimen. Reg. no. 1921:10:18:2338. Balavia. Budde-Lund Collection.

Setaphora sp.

Five specimens. Reg. no. 1921:10:18:2378-2382. Buitenzorg. Collected by K. Kraepelin. Budde-Lund Collection.

Setaphora sp.

Seven specimens. Reg. no. 1921:10:18:2384-2390. Botanical Gardens, Kew, Surrey. Collected by Bagnall. Budde-Lund Collection.

INCERTAE SEDIS

Genus 1

Species *a*

One specimen. Reg. no. 1921:10:18:5691. Paraguay. Budde-Lund Collection.

Species *b*

Two specimens. Reg. no. 1921:10:18:2165-2166. La Moka. February 1891. Budde-Lund Collection.

Species *c*

One specimen. Reg. no. 1921:10:18:5690. Paraguay. Budde-Lund Collection.

Species *d*

Six specimens. Reg. no. 1921:10:18:5692-5697. Paraguay. Budde-Lund Collection.

Species *e*

Two specimens. Reg. no. 1921:10:18:5698-5699. Corral, Chile. 5.7.1893. Budde-Lund Collection.

Species *f*

One specimen. Reg. no. 1921:10:18:5700. Venezuela. Budde-Lund Collection.

Genus 2

Species *a*

One specimen. Reg. no. 1931:4:27:71. Georgia. Verhoeff Collection.

Genus 3

Species *a*

One specimen. Reg. no. 1921:10:18:793. No locality. Budde-Lund Collection.

Genus 4

Species *a*

Two specimens. Reg. no. 1921:10:18:5753-5754. Ralum. 27.2.1897. Budde-Lund Collection.

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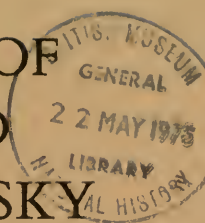
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THE LARVAL DEVELOPMENT OF
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(CRUSTACEA, BRACHYURA,
PORTUNIDAE) REARED IN THE
LABORATORY



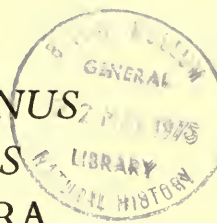
A. L. RICE
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R. W. INGLE

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BY
A. L. RICE
Institute of Oceanographic Sciences
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R. W. INGLE

Pp. 101-119 ; 1 Plate ; 8 Text-figures ; 2 Tables

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THE LARVAL DEVELOPMENT OF *CARCINUS MAENAS* (L.) AND *C. MEDITERRANEUS* CZERNIAVSKY (CRUSTACEA, BRACHYURA, PORTUNIDAE) REARED IN THE LABORATORY

By A. L. RICE AND R. W. INGLE

SYNOPSIS

The larval stages of the shore crab *Carcinus* reared from females collected in British waters are compared with those reared from a female collected in Tunisia and slight, but consistent, differences are noted between them. The Atlantic and Mediterranean populations of *Carcinus* have recently been separated as distinct species on the basis of adult characters, the name *C. maenas* (L.) being applied to the Atlantic form and *C. mediterraneus* Czerniavsky to the Mediterranean form. Although the larval differences support the possibility that the two populations are genetically distinct, if, as presently seems to be the case, they are found to be totally allopatric with no chance of interbreeding in areas of overlap, it is suggested that they should be accorded only subspecific status, a course which would reflect both their close relationship and geographical separation.

INTRODUCTION

IN THE first half of this century the larval stages of the crabs of north-western Europe were better known than those of any other region, mainly as a result of Lebour's (1928) classic work on the Plymouth Brachyura. Lebour's descriptions, however, were often inadequate and more recent studies on crabs from other areas, and particularly those based on reared material, have provided more detailed accounts of the larval development than those available for British species.

In 1969 therefore, a research programme was started at the British Museum (Natural History) with the intention of rearing as many British crabs as possible and providing detailed descriptions of all their developmental stages. As a result of this programme descriptions of the sponge crab *Dromia personata* (L.), and of the masked crab *Corystes cassivelaunus* (Pennant), have already been published (Rice, Ingle & Allen, 1970; Ingle & Rice, 1971) and although crabs of any of the fourteen families represented in British waters will be reared and described as and when ovigerous females become available, efforts are now being concentrated on the swimming crab family Portunidae and the spider crab family Majidae and the programme has been expanded to include the rearing of Mediterranean species belonging to these families.

Apart from the spider crabs (Majidae) the portunids are better represented around British coasts than any other family of crabs, fourteen species and five genera having been recorded. This paper deals with the commonest of these species, *Carcinus maenas* (L.) and with the closely related Mediterranean form, *C. mediterraneus* Czerniavsky.

The common shore crab or green crab, *C. maenas*, is found in the Atlantic on all types of shore and sublittoral to depths of 200 m, from northern Norway to

Mauritiana in the east and from Nova Scotia to Brazil in the west (Christiansen, 1969). It is therefore not surprising that it was one of the first crabs to have its development investigated, the first zoea having been hatched and described by Couch in 1840.

Since that time there have been many accounts of the various larval stages of *Carcinus*, those by Williamson (1900, 1903) being by far the most detailed and complete (see Lebour, 1928, for earlier references). Williamson hatched the first zoea which moulted to the second stage, but he obtained the later zoeae and the megalopa from the plankton and it was not until 1967 that the species was reared in the laboratory with any degree of success (Williams, 1967). Williams, however, reared *Carcinus* mainly for behavioural studies and did not describe the larval stages which she obtained, so that there is still no published account of the species' development based on reared material.

In 1971 we succeeded in obtaining all four zoeae, the megalopa and the young crab stages of *Carcinus maenas* from laboratory-reared material. At that time *Carcinus* was being used simply as a test animal to assess the efficiency of the rearing method, the shore crab having been chosen for this purpose because of the relative ease with which ovigerous females could be obtained. Compared with many other British crabs the larvae of *C. maenas* were well known and a new account did not seem to be warranted, even though the description could now be based on a complete series of reared stages. However, Williamson's papers were published in a journal which is not now readily accessible to many workers and when one of us (R. W. I.) reared the larval stages of *C. mediterraneus* from a female collected in Tunisian waters, it seemed worth while to publish a comparative account of the development of these two closely related species.

MATERIAL AND METHODS

Larvae were reared from two female *Carcinus maenas*, one collected at Plymouth, Devon, in April 1971 (B.M. reg. no. 1974:331) and the other at Brighton, Sussex, in May 1973 (B.M. reg. no. 1974:332), and from one female *C. mediterraneus* collected at the northern Punic Port, Salammbo, Tunis in February 1974 (B.M. reg. no. 1974:330).

The ovigerous crabs were maintained in sea water treated with 0.01 N EDTA and in each case hatching occurred over a 48 h period. All larvae were reared at 15 °C (but see below) in sea water treated with EDTA (0.01 N), benzylpenicillin (50 000 units/litre) and reduced glutathione (0.001 M), the last additive acting as a feeding stimulant. Every other day the culture water was changed and at the same time the larvae were fed on freshly hatched *Artemia* nauplii.

The Plymouth *C. maenas* larvae were reared in compartmented plastic trays, while the Brighton *C. maenas* and the *C. mediterraneus* were reared in 'mass culture' polythene jars using a technique similar to that described by Cook (1969) for rearing penaeid larvae. In these cases 300–400 larvae were placed into each container (see Fig. 1) and the large *Artemia* moults and dead larvae were removed when the water

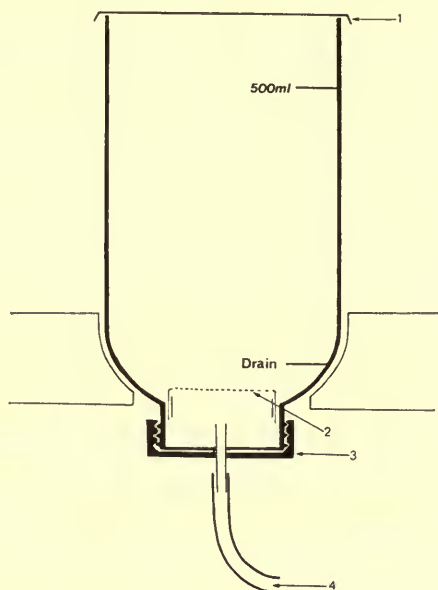


FIG. 1. Mass-culture vessel made from a 500 ml polythene bottle and used to rear *Carcinus*. 1, lid; 2, nylon mesh secured by a collar; 3, screw-on jar cap; 4, air supply and drain tube.

level was reduced to the 'drain' line at each water change. A gentle air stream induced sufficient water movement in the jars to keep the larvae circulating.

Survivals of both the tray-reared and mass-cultured *C. maenas* larvae were very high, up to 68 per cent of the stage 1 zoeae reaching the first crab stage. During the *C. mediterraneus* culture period, however, an air-conditioner breakdown resulted in several days of oscillating water temperatures reaching 25 °C. Survivals were therefore poor, only two animals reaching the first young crab stage and neither surviving to the next moult.

The larvae and moults were preserved in 70 per cent ethanol, and cleared and dissected in lactic acid. Drawings and measurements were made with the aid of a *camera lucida*. The measurements taken were (a) the distance between the tips of the dorsal and rostral spines (*T.T.*), (b) the rostral spine length (*R.S.*) from the tip of the spine to the lower margin of the eye, (c) the dorsal spine length (*D.S.*) and (d) the carapace length (*C.L.*) from between the eyes to the postero-lateral carapace margin.

RESULTS

Adults

Until relatively recently the genus *Carcinus* was considered to contain only the single species, *C. maenas*, which was recorded from the Atlantic, the Mediterranean and, probably as an introduced form, from the Indo-West Pacific region.

Demeusy & Veillet (1953) pointed out differences between the Atlantic and Mediterranean populations and Holthuis & Gottlieb (1958) resurrected the name *C. mediterraneus* Czerniavsky for the Mediterranean form.

Four of the features mentioned by Zariquiy Alvarez (1968) as distinguishing *C. mediterraneus* adults from those of *C. maenas*, that is the less sharp antero-lateral carapace teeth, the denser setation of the antero-lateral carapace margins, the sharper carpal tooth on the cheliped and the more pronounced antero-external angle of the merus of the third maxilliped, are not apparent in the females from which the larvae reported in this paper were obtained. There are, nevertheless, good morphological distinctions between the females and these are listed in Table 1 and illustrated in Plate 1.

TABLE 1

Differences between the female *C. maenas* and *C. mediterraneus* from which the larvae were reared (see also Plate 1)

<i>C. maenas</i>	<i>C. mediterraneus</i>
1. Carapace relatively broad (Brighton spec. <i>C.L.</i> 29.5 mm, <i>C.W.</i> 39.0 mm, <i>C.W./C.L.</i> 1.32; Plymouth spec. <i>C.L.</i> 40.0 mm, <i>C.W.</i> 51.5 mm, <i>C.W./C.L.</i> 1.29) (Plate 1A)	Carapace relatively narrow (<i>C.L.</i> 27.55 mm, <i>C.W.</i> 34.5 mm, <i>C.W./C.L.</i> 1.25) (Plate 1D)
2. Carapace dorsal surface relatively rough to touch	Carapace dorsal surface smooth
3. 5th (posterior) pair of antero-lateral teeth directed forwards	5th pair of antero-lateral teeth directed more or less outwards
4. Front does not protrude and is not setose (Plate 1A)	Front protrudes and is setose (Plate 1D)
5. Carapace regions not strongly elevated and, when viewed from behind, carapace relatively flat (Plate 1B)	Carapace regions elevated, and carapace vaulted (Plate 1E)
6. Outer margin of cheliped carpus not setose (Plate 1C)	Outer margin of cheliped carpus setose (Plate 1F)

Larval stages

The larvae of the two forms are very similar, particularly in the zoeal stages where the only morphological distinctions noted were the relative lengths of the dorsal and rostral carapace spines. With the exception of the dimensions, therefore, the following descriptions of the zoeae apply both to *C. maenas* and *C. mediterraneus*.

FIRST ZOEAE

Dimensions

Carcinus maenas: *T.T.* 1.36–1.44 mm, mean (10 specimens) 1.38 mm; *C.L.* 0.47–0.53 mm, mean 0.50 mm; *D.S.* 0.53–0.57 mm, mean 0.55 mm; *R.S.* 0.46–0.51 mm, mean 0.49 mm; ratio *D.S./R.S.* 1.04–1.22, mean 1.12.

Carcinus mediterraneus: *T.T.* 1.36–1.43 mm, mean (10 specimens) 1.38 mm; *C.L.* 0.53–0.57 mm, mean 0.56 mm; *D.S.* 0.58–0.63 mm, mean 0.60 mm; *R.S.* 0.40–0.43 mm, mean 0.41 mm; ratio *D.S./R.S.* 1.34–1.57, mean 1.47.

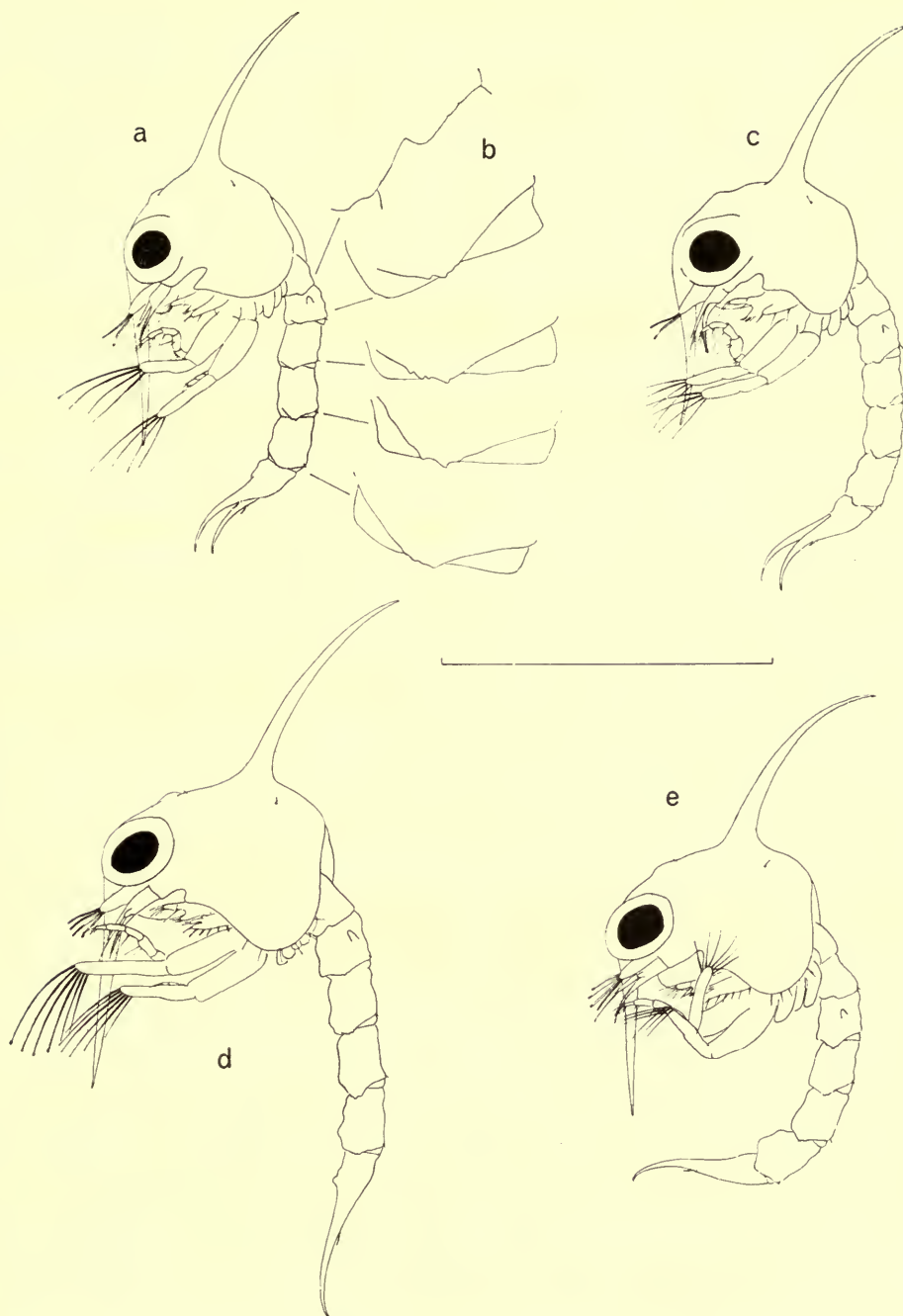


FIG. 2. *Carcinus* zoal stages I and II: (a) *C. maenas* stage I; (b) detail of postero-lateral angles of abdominal somites; (c) *C. mediterraneus* stage I; (d) *C. maenas* stage II; (e) *C. mediterraneus* stage II. Bar scale represents 1.0 mm.

Carapace (Fig. 2a, c) : Well-developed backwardly curved dorsal spine and straight or slightly curved rostral spine, but no laterals. A low anterior papilla between the eyes and a pair of small setae lateral to and slightly behind the dorsal spine.

Eyes : Partly fused to carapace.

Antennule (Fig. 3b) : Unsegmented, with two terminal aesthetascs and two setae.

Antenna (Fig. 3c) : Spinous process about half as long as rostral spine in *C. mediterraneus* and somewhat less in *C. maenas*, with two rows of spinules on the distal two-thirds. Exopod about half as long as spinous process, with one long and one short terminal spine each with minute spinules at their bases. Endopod represented by a small bud.

Mandible : Without palp.

Maxillule (Fig. 3d) : Endopod two-segmented, with 6 and 1 setae respectively. Basal endite with 4 setose spines and 1 seta, coxal endite with a total of 5 spines and setae.

Maxilla (Fig. 3e) : Endopod, basal endite and coxal endite each bilobed, with 5 + 3, 4 + 4 and 3 + 3 setae respectively. Scaphognathite with 4 marginal setae and a long plumose posterior projection.

First maxilliped (Fig. 3f) : Basis with 8 or 9 medial setae. Five-segmented endopod with 2, 2, 1, 2 and 4 + 1 setae respectively. Exopod with 4 natatory setae.

Second maxilliped (Fig. 3g) : Basis with 4 medial setae. Three-segmented endopod normally with 1, 1 and 5 setae, though the small lateral seta on the terminal segment may be absent. Exopod with 4 natatory setae.

Third maxilliped and pereopods : Unarmed, unsegmented buds.

Abdomen (Fig. 3a) : Five somites and telson. Somite 2 with forwardly directed dorso-lateral knobs. Somites 2-5 each with rounded postero-lateral margins with small teeth, and with a pair of small setae near the posterior margin. Telson with 3 pairs of setose processes on the posterior margin, and each fork with one large and one small dorsal spine and a very slender lateral spine.

SECOND ZOEAL

Dimensions

Carcinus maenas : *T.T.* 1.58-1.85 mm, mean (8 specimens) 1.75 mm ; *C.L.* 0.60-0.70 mm, mean 0.67 mm ; *D.S.* 0.55-0.70 mm, mean 0.67 mm ; *R.S.* 0.52-0.65 mm, mean 0.58 mm ; ratio *D.S./R.S.* 1.06-1.26, mean 1.15.

Carcinus mediterraneus : *T.T.* 1.44-1.56 mm, mean (7 specimens) 1.46 mm ; *C.L.* 0.60-0.70 mm, mean 0.62 mm ; *D.S.* 0.58-0.63 mm, mean 0.59 mm ; *R.S.* 0.36-0.48 mm, mean 0.43 mm ; ratio *D.S./R.S.* 1.30-1.69, mean 1.38.

Carapace (Fig. 2d, e) : A pair of small setae added between the dorsal spine and the anterior papilla. Postero-lateral margins with 4-6 setae. Otherwise as in the first stage.

Eyes : Now stalked.

Antennule (Fig. 3h) : Unsegmented, with 4-6 terminal aesthetascs and 1 or 2 setae.

Antenna (Fig. 3j) : Endopod bud slightly larger than in first stage, otherwise unchanged.



FIG. 3. *Carcinus* zoeal stages I and II: (a) abdomen, stage I; (b) antennule, stage I; (c) antenna, stage I; (d) maxillule, stage I; (e) maxilla, stage I; (f) first maxilliped, stage I; (g) second maxilliped, stage I; (h) antennule, stage II; (i) antenna, stage II; (j) maxillule, stage II; (k) maxilla, stage II; (l) maxilla, stage II. Appendages b, c, e, k and l are drawn from *C. maenas* specimens and the remainder from *C. mediterraneus*. Bar scale represents 0.2 mm for a, f and g, and 0.1 mm for the rest.

Mandibles : Unchanged.

Maxillule (Fig. 3*k*) : Basal endite with 6 or 7 spines and setae, coxal endite with 5 or 6. Exopod seta now present, endopod unchanged.

Maxilla (Fig. 3*l*) : Scaphognathite now with 9-11 marginal setae, the posterior projection no longer being apparent. Endopod and basal endites unchanged, but coxal endite may now carry an extra seta.

First and second maxilliped (Fig. 2*d, e*) : Exopods with 6 natatory setae ; otherwise unchanged.

Third maxilliped and pereopods : Still unsegmented and unarmed buds.

Abdomen : Unchanged except that the two smaller spines on each telson fork are either reduced or absent.

THIRD ZOEAE

Dimensions

Carcinus maenas : *T.T.* 2.13-2.15 mm, mean (3 specimens) 2.14 mm ; *C.L.* 0.79-0.85 mm, mean 0.82 mm ; *D.S.* 0.80-0.85 mm, mean 0.82 mm ; *R.S.* 0.70-0.80 mm, mean 0.73 mm ; ratio *D.S./R.S.* 1.06-1.21, mean 1.14.

Carcinus mediterraneus : *T.T.* 1.93 mm ; *C.L.* 0.82 mm ; *D.S.* 0.77 mm ; *R.S.* 0.51 mm ; ratio *D.S./R.S.* 1.52.

Carapace (Fig. 4*a, b*) : Postero-lateral margins with 8-12 setae, otherwise unchanged.

Antennule (Fig. 4*d*) : Three or four terminal and one sub-terminal aesthetascs, plus 1 or 2 terminal setae.

Antenna (Fig. 4*e*) : Exopod about two-thirds length of spinous process ; endopod slightly shorter.

Maxillule (Fig. 4*f*) : Basal and coxal endites with 9 and 6 spines respectively ; 1 or 2 exopod setae ; endopod unchanged.

Maxilla (Fig. 4*g*) : Endopod, basal endite and coxal endite with 4-5+3, 3-5+4 and 3-4+3 setae respectively. Scaphognathite with 19 or 20 marginal setae.

First maxilliped (Fig. 4*a, b*) : Basis and endopod unchanged except that terminal segment may carry 4 or 5+1 seta ; exopod with 8 natatory setae.

Second maxilliped (Fig. 4*a, b*) : Exopod with 8 natatory setae ; otherwise unchanged.

Third maxilliped : Now bilobed, but still unsegmented and unarmed.

Pereopods : Unarmed, unsegmented buds, first pair cheliform.

Abdomen (Fig. 4*a, b*) : Somite 1 with single median dorsal seta, somites 2-5 with well-developed pleopod buds, somite 6 separated from the telson and carrying small uropod buds. Telson forks each usually with one large and one small dorsal spine, though the latter may be absent.

FOURTH ZOEAE

Dimensions

Carcinus maenas : *T.T.* 2.20-2.50 mm, mean (5 specimens) 2.37 mm ; *C.L.* 1.02-1.10, mean 1.06 mm ; *D.S.* 0.81-0.91, mean 0.86 mm ; *R.S.* 0.74-0.83 mm, mean 0.77 mm ; ratio *D.S./R.S.* 1.02-1.20, mean 1.11.

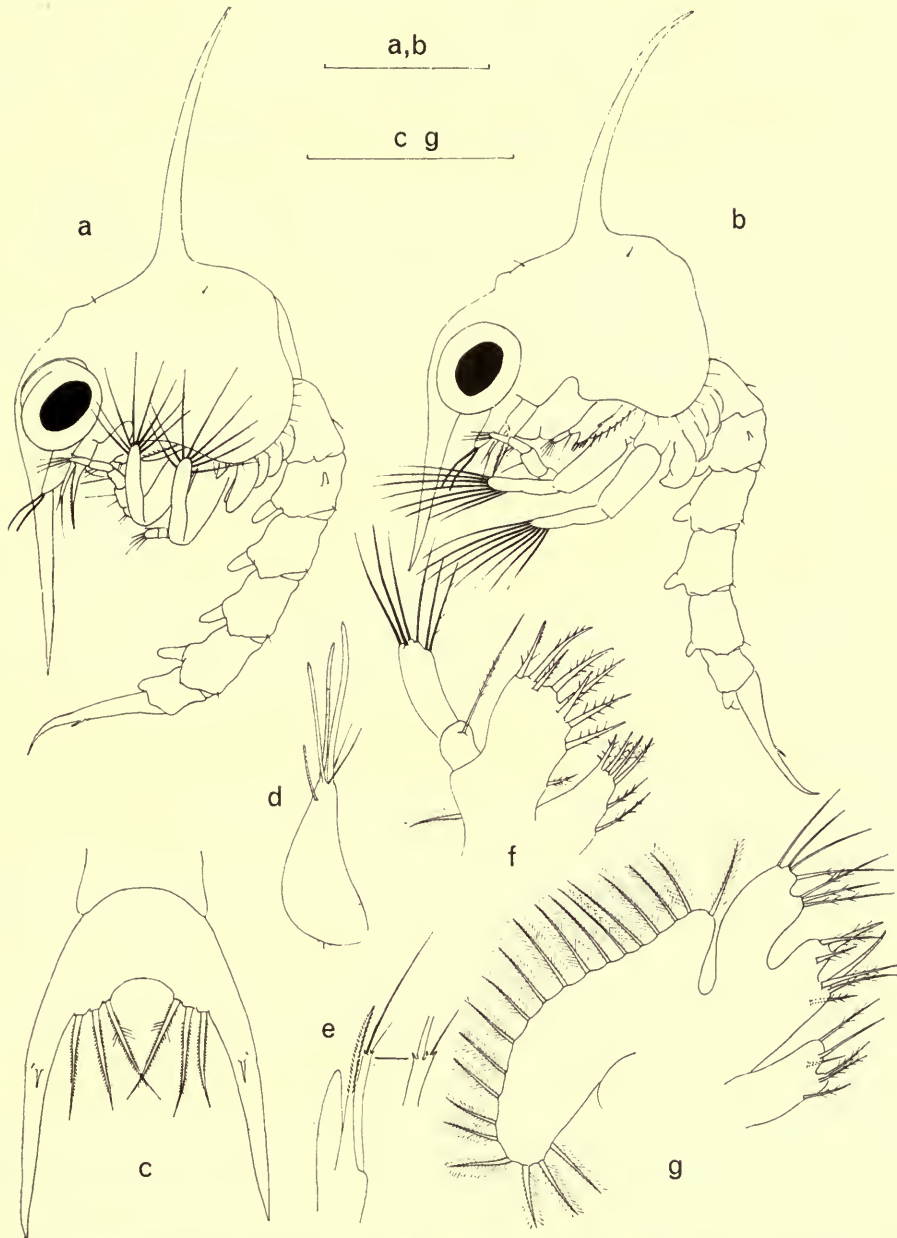


FIG. 4. *Carcinus* zoea stage III : (a) *C. maenas* ; (b) *C. mediterraneus* ; (c) telson, *mediterraneus* ; (d) antennule, *maenas* ; (e) antenna, *maenas* ; (f) maxillule, *mediterraneus* ; (g) maxilla, *mediterraneus*. Bar scales represent 0.5 mm for a and b and 0.25 mm for c-g.

Carcinus mediterraneus : *T.T.* 2.10–2.35 mm, mean 2.23 mm ; *C.L.* 0.90–0.99 mm, mean 0.95 mm ; *D.S.* 0.90–0.95 mm, mean 0.93 mm ; *R.S.* 0.67–0.72 mm, mean 0.70 mm ; ratio *D.S./R.S.* 1.32–1.34, mean 1.33.

Carapace (Fig. 5a, b) : Postero-lateral margin now with 12–16 setae, otherwise unchanged.

Antennule (Fig. 5d) : Terminal seta and a total of 6–7 aesthetascs in three groups. Exopod bud present.

Antenna (Fig. 5e) : Endopod now equal or almost equal to spinous process.

Maxillule : Basal endite may have an additional spine, otherwise unchanged.

Maxilla (Fig. 5f) : Scaphognathite with 22–24 marginal setae. Setation of endopod and endites falls within the range in the third stage.

First and second maxillipeds : Exopods with 10 natatory setae, otherwise unchanged.

Third maxilliped and pereopods : Large and with the beginnings of segmentation, but still unarmed.

Abdomen (Fig. 5a, b and c) : Pleopods now as long as succeeding abdominal somites. Telson forks with one large dorsal spine and usually with a minute second spine.

MEGALOPA

The megalopa stages of the two species are more easily distinguished than the zoeae. However, the differences noted involve only the pleopods, uropods and telson and with the exception of these features the following description, like those of the zoeal stages, applies both to *C. maenas* and *C. mediterraneus*.

Dimensions

Carcinus maenas : *C.L.* 1.26–1.40 mm ; *C.W.* 0.96–1.18 mm.

Carcinus mediterraneus : *C.L.* c 1.21 mm ; *C.W.* c 1.02 mm.

Antennule (Fig. 7a) : Dorsal flagellum of 4 segments, the distal 3 segments each with 3 or 4 aesthetascs. Terminal segment with 2 setae, penultimate segment with a lateral seta and with or without a medial seta. Ventral flagellum unsegmented with 4 terminal setae, and 1 or 2 subterminal ones.

Antenna (Fig. 7b) : Three-segmented peduncle carrying 3, 0 and 1 setae respectively. Flagellum of 7 segments, though the septum between segments 2 and 3 is indistinct. Flagellar segments 3, 5 and 7 each carry 4 setae.

Mandible (Fig. 7e) : Two-segmented palp with about 6 terminal setae.

Maxillule (Fig. 7c) : Endopod with 1 or 2 terminal setae ; basal endite with a row of 5–7 marginal spines and a total of about 11 setae, coxal endite with 7 or 8 setae.

Maxilla (Fig. 7d) : Scaphognathite with 37–44 marginal setae and with 5 or 6 setae on the surfaces of the blade. Endopod unarmed or with a single short seta. Lobes of the basal and coxal endites carrying 7, 6–7, 2 and 3–4 setae respectively.

First maxilliped (Fig. 7f) : Exopod two-segmented, with 2 setae on proximal segment and 3–5 on the distal segment. Unsegmented endopod with 4 or 5 marginal setae. Basal segment with 14–16 marginal and sub-marginal setae. Coxal endite with 5 or 6 setae. Well-developed triangular epipod.



FIG. 5. *Carcinus* zoea stage IV: (a) *C. maenas*; (b) *C. mediterraneus*; (c) telson, *maenas*; (d) antennule, *maenas*; (e) antenna, *maenas*; (f) maxilla, *mediterraneus*. Bar scales represent 0.5 mm for a and b., 0.25 mm for c, d and e, and 0.1 mm for f.

Second maxilliped (Fig. 7g): Exopod two-segmented, with 4 or 5 terminal setae. Endopod of 5 segments, the proximal unarmed. Epipod bilobed.

Third maxilliped (Fig. 7h): Exopod two-segmented, with 4 terminal setae. Endopod of 5 segments, armed with numerous spines and setae and with the ischium expanded and carrying 4 or 5 teeth on the medial margin. Elongated epipod with 2 gill buds.

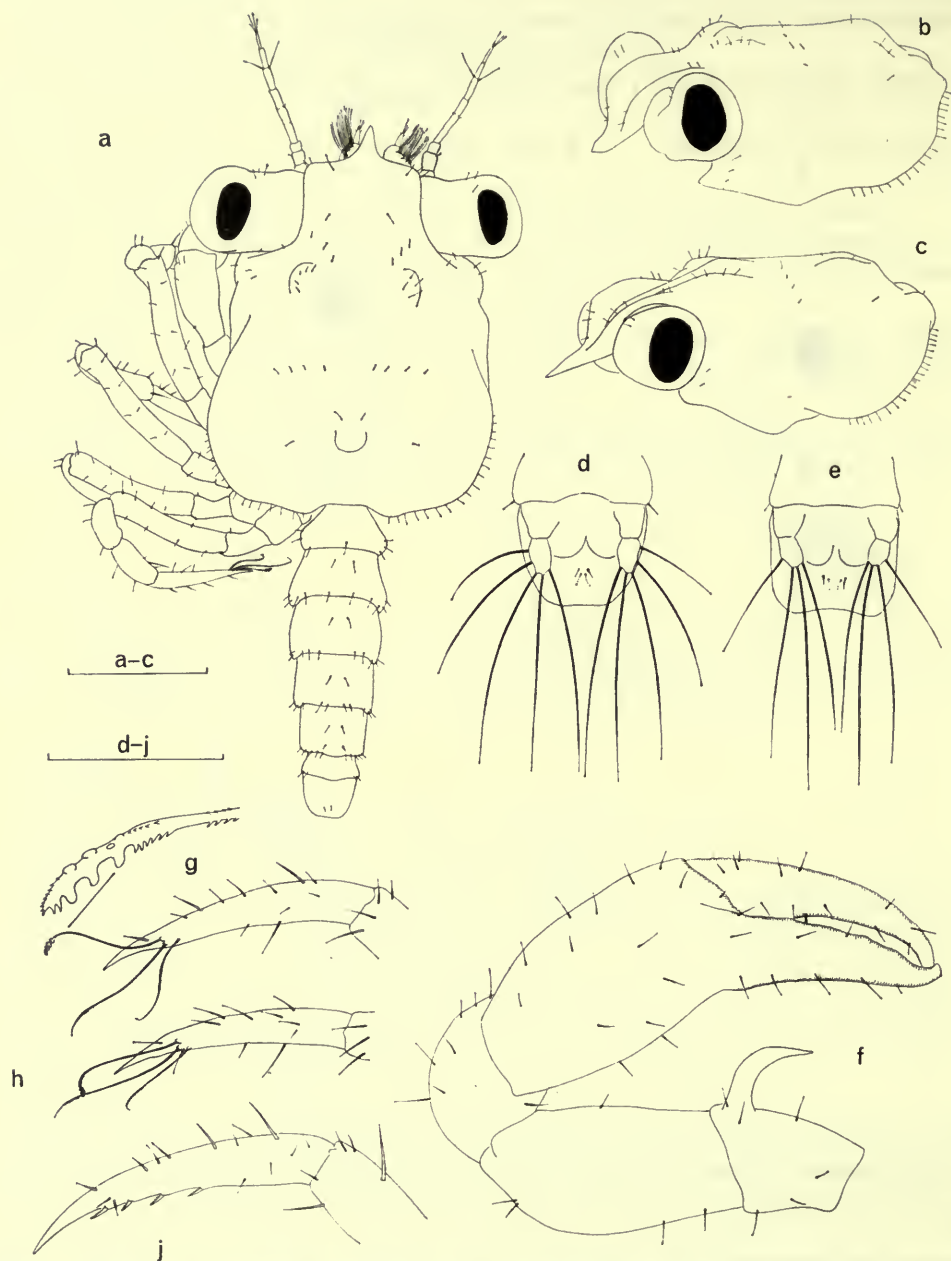


FIG. 6. *Carcinus megalopa*: (a) dorsal view, *C. maenas*; (b and c) anterior-lateral views of carapace in *C. maenas* (b) and *C. mediterraneus* (c); (d and e) ventral views of telson and uropods in *C. maenas* (d) and *C. mediterraneus* (e); (g and h) dactyl of fifth pereiopod in *C. maenas* (g) and *C. mediterraneus* (h); (j) dactyl of second pereiopod, *C. maenas*; (f) cheliped, *C. maenas*. Bar scales represent 0.55 mm for a-c, and 0.25 mm for d-j.

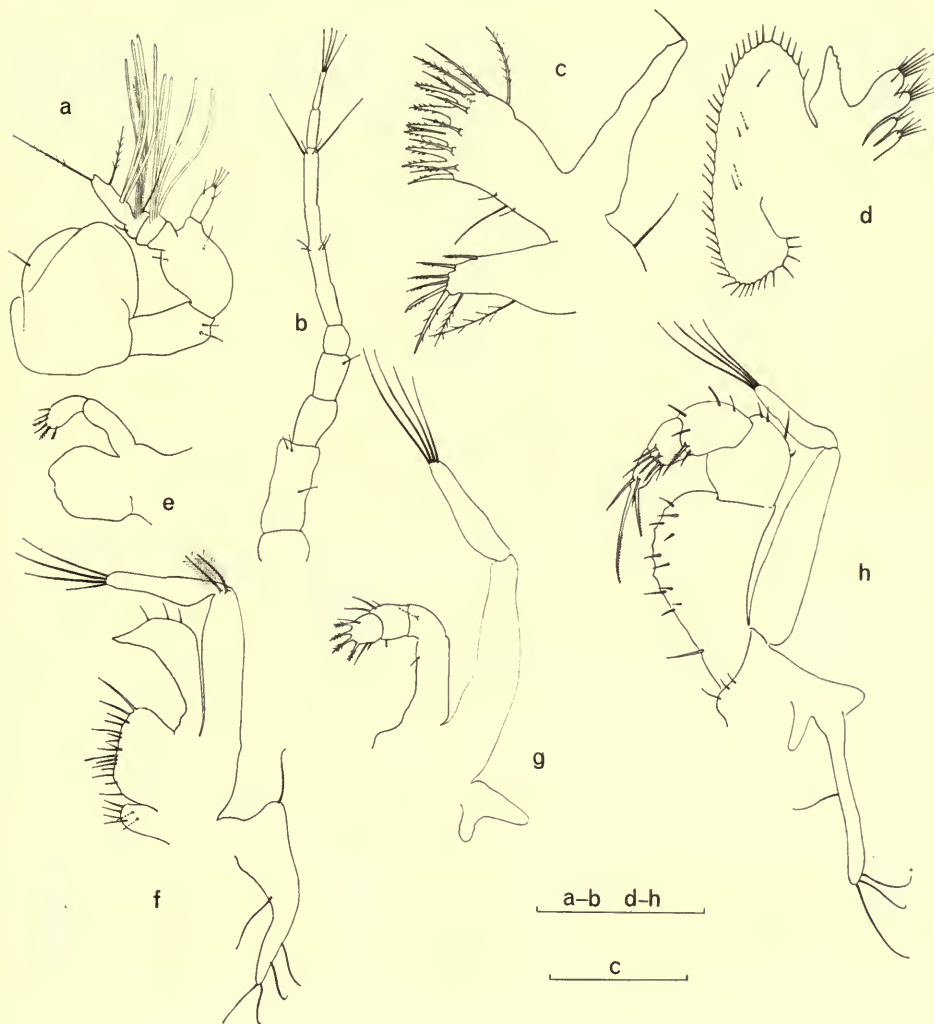


FIG. 7. *Carcinus maenas* megalopa; (a) antennule; (b) antenna; (c) maxillule; (d) maxilla; (e) mandible; (f) first maxilliped; (g) second maxilliped; (h) third maxilliped. Bar scales represent 0.1 mm for (c) and 0.25 mm for the remainder.

Pereiopods (Fig. 6a and f-j): Chelipeds with prominent ischio-basal hook. Legs 2-5 without coxal spines. Dactyl of leg 5 narrow (length/width ratio about 7:1), with 3 long, sub-terminal sensory setae.

Abdomen (Fig. 6a, d and e): Somites 2-4 with slightly variable pattern of dorsal setae, but usually with 5 pairs on the postero-dorsal margin and 1 pair more anteriorly. Somite 5 with an extra pair. Telson with a pair of setae on both the dorsal and ventral surfaces, somewhat variable in shape, but with consistent differences between the two forms; in *C. maenas* the telson narrows posteriorly and

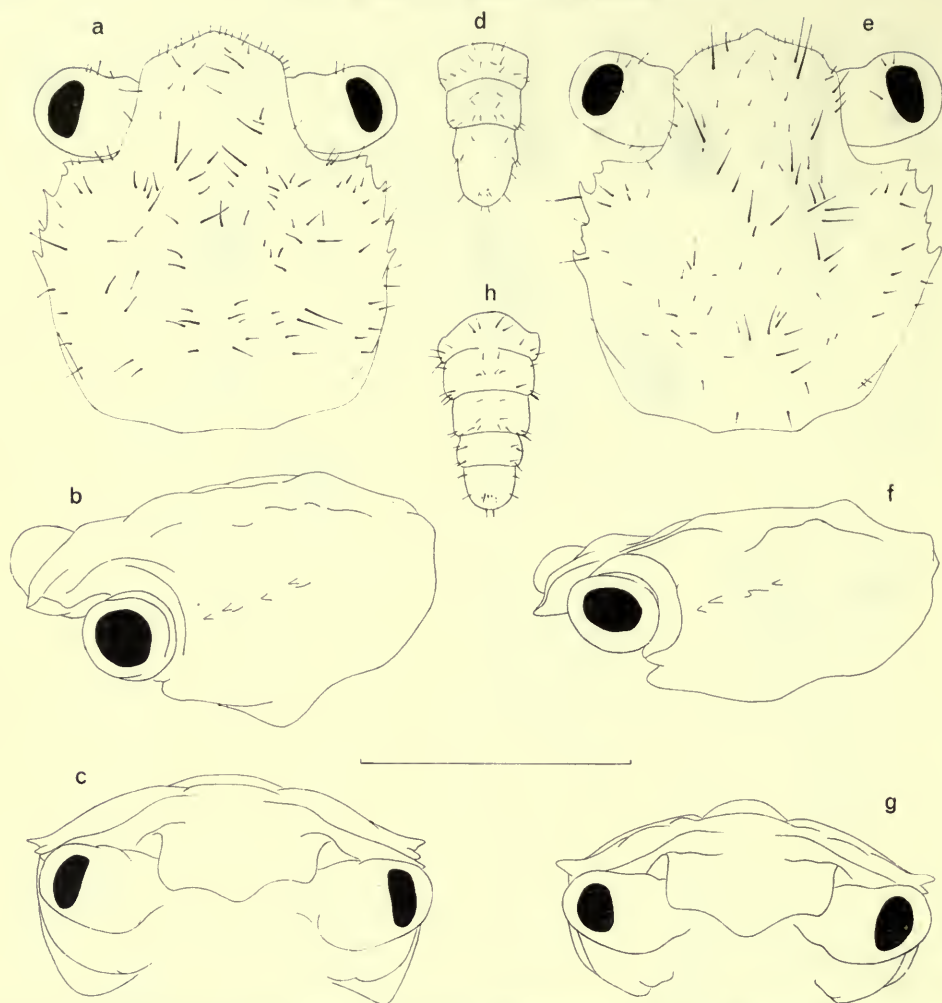


FIG. 8. *Carcinus* first crab stage : (a-d) *Carcinus maenas*, (e-h) *C. mediterraneus*, carapace (dorsal, lateral and frontal views) and abdomen. Bar scale represents 1.0 mm.

the posterior margin is usually straight or convex, and rarely concave ; in *C. mediterraneus* it is much more square, the lateral margins being more or less parallel or even diverging slightly, the postero-lateral angles are more abrupt and the posterior margin is always concave, often markedly so.

Pleopods and uropods (Fig. 6d, e) : In both *C. maenas* and *C. mediterraneus* the pleopods are well developed with 3, rarely 4, coupling hooks on each endopod. But the setation of the exopods of these appendages and of the uropods was consistently different in the examples of the two forms examined and afforded the clearest means of separation. In general *C. mediterraneus* had fewer setae on the pleopods than did *C. maenas*, though since there was a good deal of overlap the setation of no single appendage would separate the two forms (see Table 2). When, however, the total

number of setae on the pleopods of the 5th abdominal somite and on the uropods was combined, a clear distinction was apparent, *C. maenas* megalopae always having a total of 32 setae on these appendages, while *C. mediterraneus* larvae never had more than 30.

TABLE 2

Setation of the pleopods and uropods in the megalopa larvae of *C. maenas* and *C. mediterraneus*, based on counts of five specimens in each case

	<i>C. maenas</i>		<i>C. mediterraneus</i>	
	Range	Mean	Range	Mean
Pleopod, somite 2	10-12	11.0	11-13	11.1
somite 3	11-12	11.9	11-12	11.8
somite 4	12-13	12.4	11-12	11.3
somite 5	11	11	9-11	9.8
Uropod	5	5	4-6	4.5

FIRST CRAB STAGE (Fig. 8)

Carcinus maenas: Carapace length 1.49-1.52 mm; carapace width (across tips of 5th antero-lateral carapace spines) 1.36-1.47 mm.

Carcinus mediterraneus: Carapace length 1.49-1.57 mm; carapace width 1.38-1.50 mm.

Only two specimens of the first crab stage of *C. mediterraneus* were obtained so that little reliance can be placed on their comparison with the corresponding stage in *C. maenas*. However, in the material examined the two forms were extremely similar, the only differences being a slightly more prominent rostrum and dorsal carapace tubercles and a squarer telson in *C. mediterraneus* than in *C. maenas*. The other characters distinguishing the adults were not apparent in the first crab stage although *mediterraneus* has a slightly lighter build, the carapace being relatively a little narrower, than *maenas*.

DISCUSSION

Williamson's (1903) account of the development of *Carcinus maenas* includes a great deal of detail and, in this respect, has rarely been equalled by any subsequent description of decapod larvae. His larvae were generally a little larger than those reared from the Plymouth and Brighton females reported here, but otherwise the two accounts agree almost without exception. This agreement confirms, if such confirmation was needed, firstly the accuracy of Williamson's observations and secondly that his specimens of the third and fourth zoeal stage and of the megalopa, all of which he obtained from the plankton, were correctly identified. Lebour's (1928) account is much less complete, but where comparisons are possible her descriptions also agree with the reared British larvae. Both of these authors mention the loss in the late zoeae of two of the three telson fork spines which are present in the early stages, whereas a second spine was almost always present in our stage four larvae. However, this second spine is extremely small and difficult to see, so that it was probably simply missed by Williamson and Lebour.

The earlier accounts also agree with the present description of the British *Carcinus* larvae in those features which distinguish them from the Mediterranean material,

and particularly in the setation of the abdominal appendages of the megalopa. Williamson, for instance, gives the setation of the exopods of the pleopods as 11, 11-13, 12 or 13, and 11 respectively, while both he and Lebour report 5 setae on the uropods as opposed to the 4 setae usually found on our Mediterranean larvae. The account of these Mediterranean larvae is based on material obtained from only one brood so that the distinctions noted might simply reflect individual variation. But the agreement between all the available descriptions of British larvae argues against this and suggests that definite genetic differences exist between the Atlantic and Mediterranean *Carcinus* populations.

Whether these differences are sufficient to warrant the two populations being accorded full specific status is, however, debatable, for they appear to be allopatric, *C. mediterraneus* never having been reported from outside the Mediterranean, while *C. maenas* is not known from within it. In these circumstances the ultimate criterion of the absence of interbreeding between overlapping populations cannot be applied and any opinion about their taxonomic status must be somewhat subjective.

Comparing the degree of difference between the two allopatric forms with that between undoubtedly distinct species in the same group does not provide very conclusive evidence. For although portunid crabs are often quite difficult to separate as juveniles, there are usually more distinct differences between the mature forms than those noted between *Carcinus maenas* and *C. mediterraneus*, and in the larval stages the situation is similar. In terms of the number of species of which larvae have been described, the best known portunid genus is *Macropipus*, and although the known larval stages of this genus are all very similar, detailed examination has generally revealed better distinctions between the species than those between the two types of *Carcinus* larvae described here (Rice & Ingle, 1975).

It seems, then, that there is no very good larval evidence to support the separation of *maenas* and *mediterraneus* as distinct species, despite the existence of consistent differences between the adults. A study of both adults and larvae from the vicinity of the Straits of Gibraltar, both in the Mediterranean and in the Atlantic, would be of considerable interest, though if no area was found in which the two forms co-exist, or intergrade, the problem would still be unresolved. Since the adults are so readily distinguishable, however, it seems worth while at present to maintain their specific status, but if they are ultimately shown to be totally allopatric the most sensible course would probably be to consider them to be subspecies, as was apparently the intention of Czerniavsky (1884) when he divided *C. maenas* into the two varieties *mediterranea* and *septentrionalis* (see Holthuis & Gottlieb, 1958). For as Mayr, Linsley & Usinger (1953) point out, the use of trinomials has the advantage in such situations of conveying the important information that the two forms are closely related and geographically separated.

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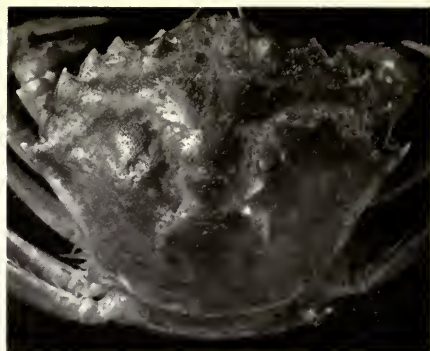
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PLATE I

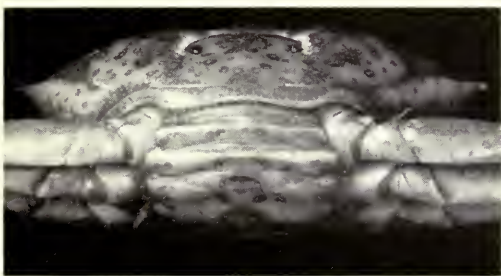
Dorsal and posterior views of the carapace and of the outer face of the right cheliped of the female *C. maenas* from Brighton (A, B and C) and of the female *C. mediterraneus* from Salmambo (D, E and F).



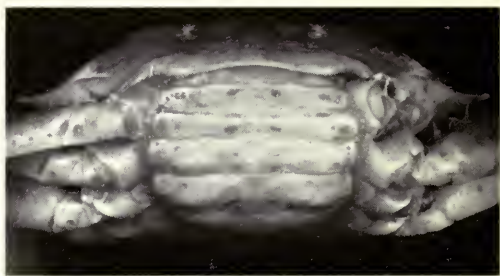
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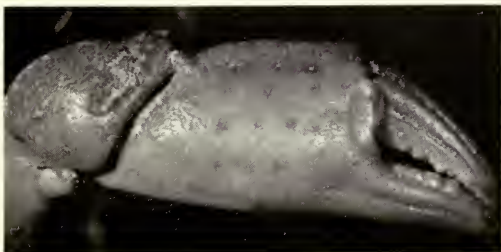
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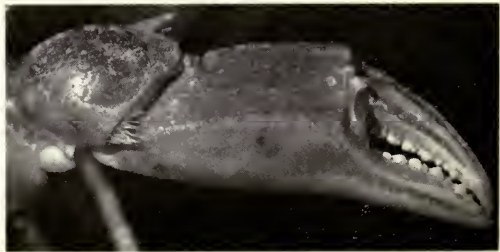
B



E



C



F



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A COMPARATIVE STUDY OF THE
LARVAL MORPHOLOGY OF THE
BRITISH PORTUNID CRABS
MACROPIPUS PUBER (L.) AND
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WITH A DISCUSSION OF GENERIC
AND SUB-FAMILIAL LARVAL
CHARACTERS WITHIN THE
PORTUNIDAE

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A. L. RICE
Institute of Oceanographic Sciences
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Pp. 121-151 ; 9 Text-figures ; 9 Tables

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A COMPARATIVE STUDY OF THE LARVAL MORPHOLOGY OF THE BRITISH PORTUNID CRABS *MACROPIPUS PUBER* (L.) AND *M. HOLSATUS* (FABRICIUS), WITH A DISCUSSION OF GENERIC AND SUB-FAMILIAL LARVAL CHARACTERS WITHIN THE PORTUNIDAE

By A. L. RICE AND R. W. INGLE

SYNOPSIS

The zoeal and megalopa stages of two portunid crabs, *Macropipus puber* and *M. holsatus*, are described from material reared in the laboratory. Comparison of these larvae with one another and with those of *M. holsatus*, the only other species of the genus described in detail, indicates that while the larvae of the *Macropipus* species are all very similar there are clear distinctions between them.

The larval information available for the family as a whole generally supports the currently accepted sub-divisions within the Portunidae based on adult characters, but further detailed larval descriptions, particularly of those sub-families of which the larval stages are at present unknown, would probably help in the interpretation of phylogenetic relationships both within the family and between the portunids and the remainder of the Brachyura.

INTRODUCTION

THIS paper is the second in what is hoped will be a series describing the larval development of the British portunid crabs. The first paper (Rice and Ingle, 1975) described larvae reared from British specimens of the shore crab, *Carcinus maenas*, and compared them with those of the closely related Mediterranean form. This second paper deals with two of the eight species of the genus *Macropipus* which have been recorded from British waters.

Although Lebour's (1928, 1944) classic work on the Plymouth Brachyura established distinctions between the larvae of several genera and species of British crabs, she was not able to separate satisfactorily the larval and young stages of the *Macropipus* species with which she dealt (under the name *Portunus*) except on the basis of chromatophore pattern. Since that time the larvae of only one species of *Macropipus* have been reared and described in detail (Goldstein, 1971), but with a further two species described here it is now possible to discuss the nature of the specific larval characters within the genus.

MATERIALS AND METHODS

The ovigerous female *Macropipus puber* was obtained from Lulworth Cove, Dorset, in September 1972 and the *M. holsatus* from Port Erin, Isle of Man, in

February 1973. In both cases the crabs were maintained in sea-water at a temperature of 15 °C and all the larvae were reared at this temperature.

The eggs of *M. puber* hatched on 25 September 1972 and those of *M. holsatus* on 27 February 1973 and both broods were reared partly in mass culture and partly individually in compartmented plastic boxes (see Rice and Ingle, 1975). All of the larvae were fed on a mixture of *Prorocentrum* and freshly hatched *Artemia* nauplii.

The survival rate through the larval stage was quite good in both species, but was somewhat better in *holsatus* than in *puber*; of 90 individually reared *M. holsatus* 25 (about 22 per cent) reached at least the first crab stage, whereas of 180 individually reared *M. puber* only 17 (about 9 per cent) reached this stage.

Although there was considerable individual variation in the number of days spent in each larval stage the total length of the larval life in both species was very similar, *M. holsatus* moulting into the first crab stage 43–53 (mean 48) days after hatching while *M. puber* reached this moult in 46–56 (mean 50) days.

The reared larvae and the females from which they were obtained are deposited in the British Museum (Natural History) under registration numbers 1974 : 333 (*M. holsatus*) and 1974 : 334 (*M. puber*).

MORPHOLOGY OF THE LARVAL STAGES AND SPECIFIC DISTINCTIONS WITHIN THE GENUS *MACROPIPUS*

The larvae of *Macropipus puber* and *M. holsatus* are illustrated in Figs. 2–9. The illustrations are supplemented in Tables 1–6 where these two species are compared with Goldstein's (1971) description of the larvae of *M. marmoreus*.

As was to be expected from previous work, the larvae of all three species are very similar, but although no single character separates them at all stages there are clear distinctions between them.

Thus the zoeae of *puber* differ from the other species at all stages in having straight rather than curved dorsal and rostral spines, and in the early stages by being considerably larger (Fig. 1A–C). This size difference becomes less marked in the later stages but at this time, that is in the fourth and fifth stages, an obvious distinction is the loss in *puber* of one of the spines on the telson forks. The larvae of *puber* are also consistently relatively narrower than those of *holsatus* and, at least in stage I, of *marmoreus* too (Fig. 1D). The absence of the relevant width data in Goldstein (1971) precludes the inclusion of *marmoreus* in this comparison beyond the first stage, specimens of which are deposited in the British Museum (Natural History).*

As in the adults (see Christiansen, 1969), the larvae of *holsatus* and *marmoreus* are more difficult to separate on morphological grounds, both of them having curved carapace spines and being similar in size. However, there are a number of fairly easily seen differences. First, the postero-lateral processes on the abdominal somites are much better developed in *marmoreus* than in either *holsatus* or *puber*, particularly in the late zoeal stages. Secondly, with the possible exception of stage III, *marmoreus* resembles *puber* and differs from *holsatus* in having the spinous process

*Stage V larvae of *M. marmoreus* subsequently received from Dr Goldstein are intermediate between *puber* and *holsatus* in this respect.

of the antenna much shorter relative to the rostral spine. Finally, the lateral knobs on the third abdominal somite are lost in stage II in *marmoreus*, that is one stage earlier than in either *holsatus* or *puber*.

In addition to these characters there are less obvious differences, particularly between the zoeae of *marmoreus* on the one hand and *puber* and *holsatus* on the other, in the number of aesthetascs on the antennules and the setation of the antennae, maxillae and maxillipeds (see Tables 1-5).

The megalopae of the three species are also very similar. Although the comparative size situation is now the reverse of that in the early zoeal stages, the megalopae of *puber* tending to be smaller than those of either *holsatus* or *marmoreus*, the size ranges overlap a good deal. Similarly, while the megalopae of *holsatus* seem to have a rather lighter build than those of the other two species, this distinction is not very clear and in any case is obscured by the distortion resulting from preservation. There are, however, good distinctions between the species based on the antennae and telson. Thus, while *puber* has an antennal flagellum of seven segments and a telson with three pairs of dorsal setae, *holsatus* has eight segments in the flagellum and only two pairs of dorsal telson setae, and *marmoreus* has six segments in the antennal flagellum and four pairs of dorsal telson setae. Finally, the slender dactyl of the fifth pereopod in *puber*, with its sub-terminal sensory setae, is clearly distinguishable from the broader dactyl and terminal setae of *holsatus* and *marmoreus*.

Although the features dealt with here clearly enable the larvae of *Macropipus puber*, *M. holsatus* and *M. marmoreus* to be differentiated, it is not possible to anticipate which of these characters, if any, will be of use in distinguishing between the other species of the genus. However, the fact that such consistent differences exist, particularly between the larval stages of *holsatus* and *marmoreus* which are so similar as adults, indicates that when the larvae of these other species are described in sufficient detail similarly clear distinctions will be found between them.

GENERIC AND SUB-FAMILIAL LARVAL DISTINCTIONS WITHIN THE FAMILY PORTUNIDAE

Previous attempts to define generic and sub-familial distinctions amongst portunid larvae have been clouded by the unfortunate nomenclatural confusion surrounding this family of crabs (see Opin. Decl. Int. Commn zool. Nom. 1956, vol. 12, Opinion 394, pp. 317-336). This confusion was primarily due to the use of the name *Portunus* for two distinct genera, one mainly confined to European waters, and the other widely distributed in the tropics and sub-tropics. The International Commission's decision was to retain the name *Portunus* Weber, 1795, for the widely distributed genus, which had also been called *Neptunus* in the Mediterranean and Indo-West-Pacific, and to adopt the name *Macropipus* Prestandrea, 1833, for the European genus. These changes have had repercussions in the nomenclature of the sub-familial divisions within the Portunidae, but the situation was clarified by Stephenson and Campbell (1960) whose interpretation and nomenclature, based on adult characters, are followed here except that the sub-family name Polybiinae Ortmann, 1893, is used in place of their Macropipinae.

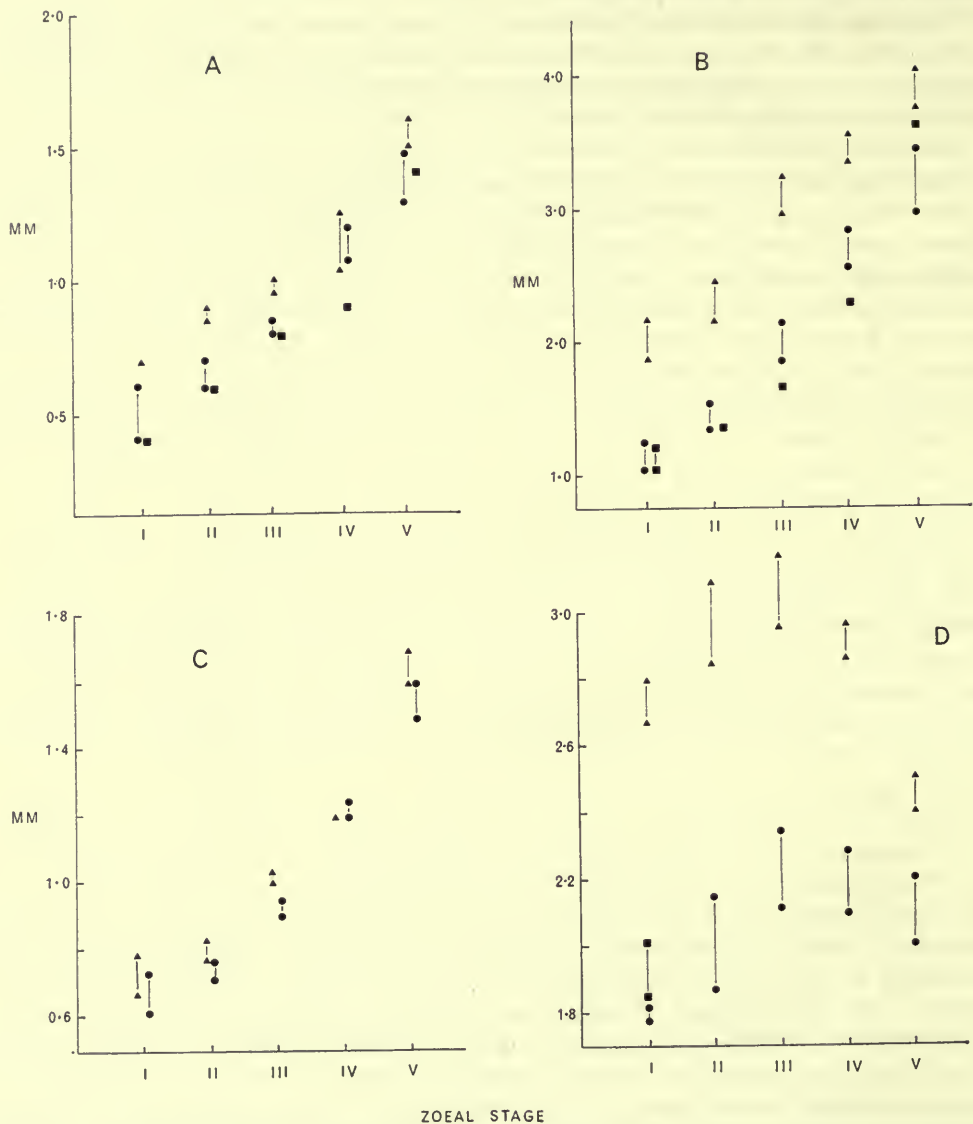


FIG. 1. A comparison of the dimensions of the zoeal stages of *Macropipus puber* (triangles), *M. holsatus* (circles) and *M. marmoreus* (squares). (A) Carapace length, (B) distance from the tip of the dorsal spine to the tip of the rostrum, (C) distance between the tips of the lateral carapace spines, and (D) ratio B/C.

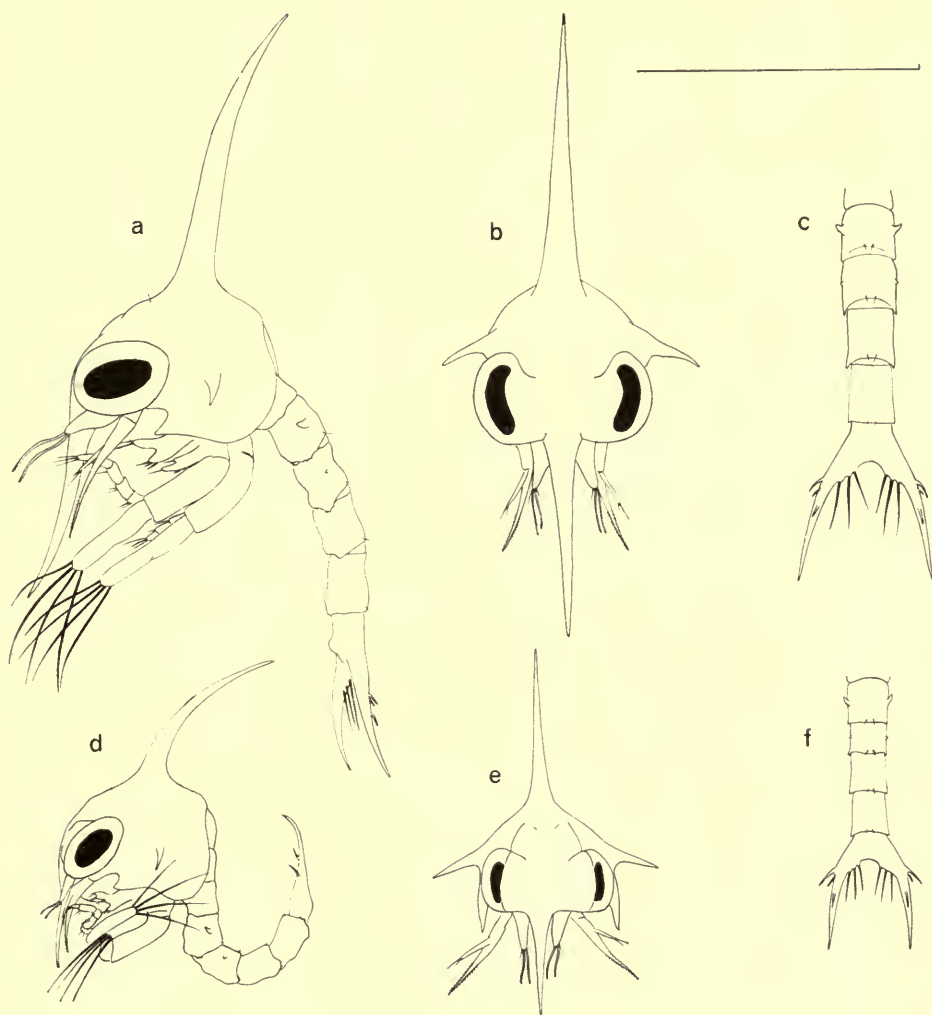


FIG. 2. First zoea of *M. puber* (a, b and c) and of *M. holsatus* (d, e and f).
The bar scale represents 1.0 mm.

Stephenson and Campbell recognized six sub-families (Carcininae, Polybiinae (= Macropipinae), Portuninae, Catoptrinae, Caphyrinae and Podophthalminae), but larvae of only the first three of these are known. Apart from *Macropipus*, larvae of only two polybiinid genera have been described in detail; *Ovalipes ocellatus* (Herbst) was reared through the zoeal stages and the megalopa by Costlow and Bookhout (1966), the megalopa of *O. punctatus* was described by Muraoka (1969), while Roberts (1969) reared *Bathynectes superba* (Costa) to the terminal zoea.

(Continued on page 142)

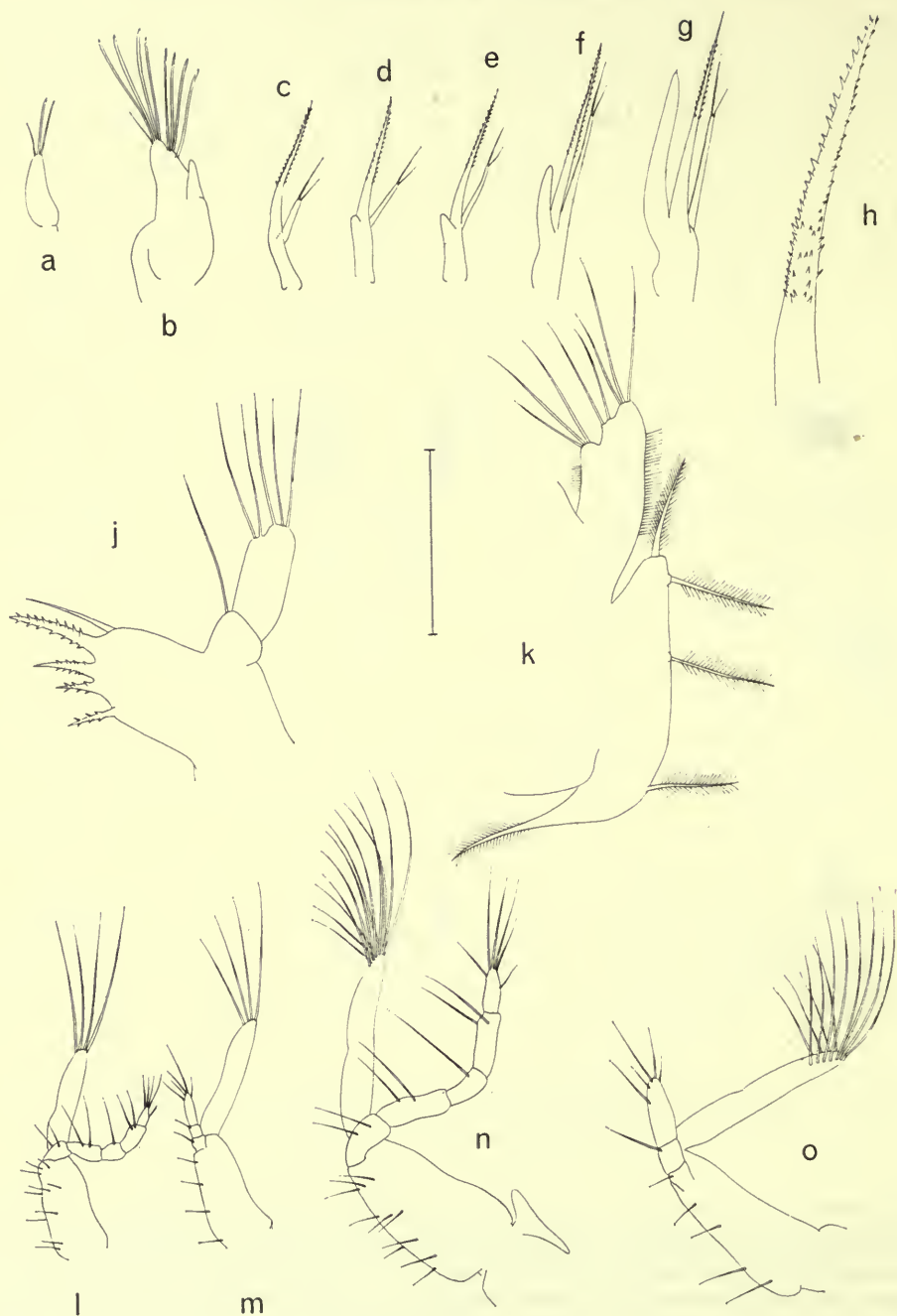


FIG. 3. Appendages of the zoeae of *M. puber*; (a) antennule, stage I, (b) antennule, stage II, (c-g) antenna, stages I-V, (h) detail of spinous process, stage I, (j) endopod and basal endite of maxillule, stage I, (k) endopod and scaphognathite of maxilla, stage II, (l and m) first and second maxillipeds, stage I, (n and o) first and second maxillipeds, stage V. The bar scale represents 0.1 mm for h, j and k, and 0.5 mm for the remainder.

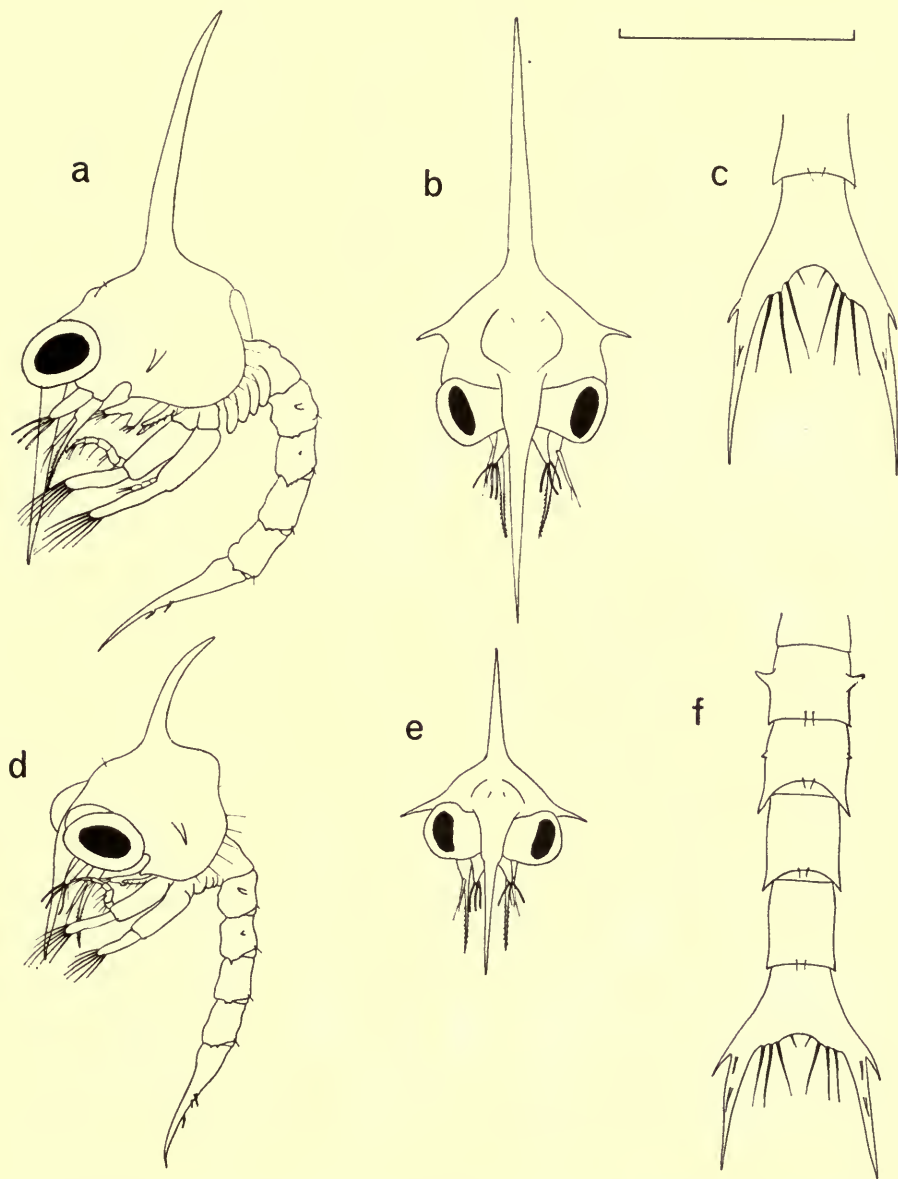


FIG. 4. Second zoea of *M. puber* (a, b and c) and of *M. holsatus* (d, e and f).
 The bar scale represents 1.0 mm.

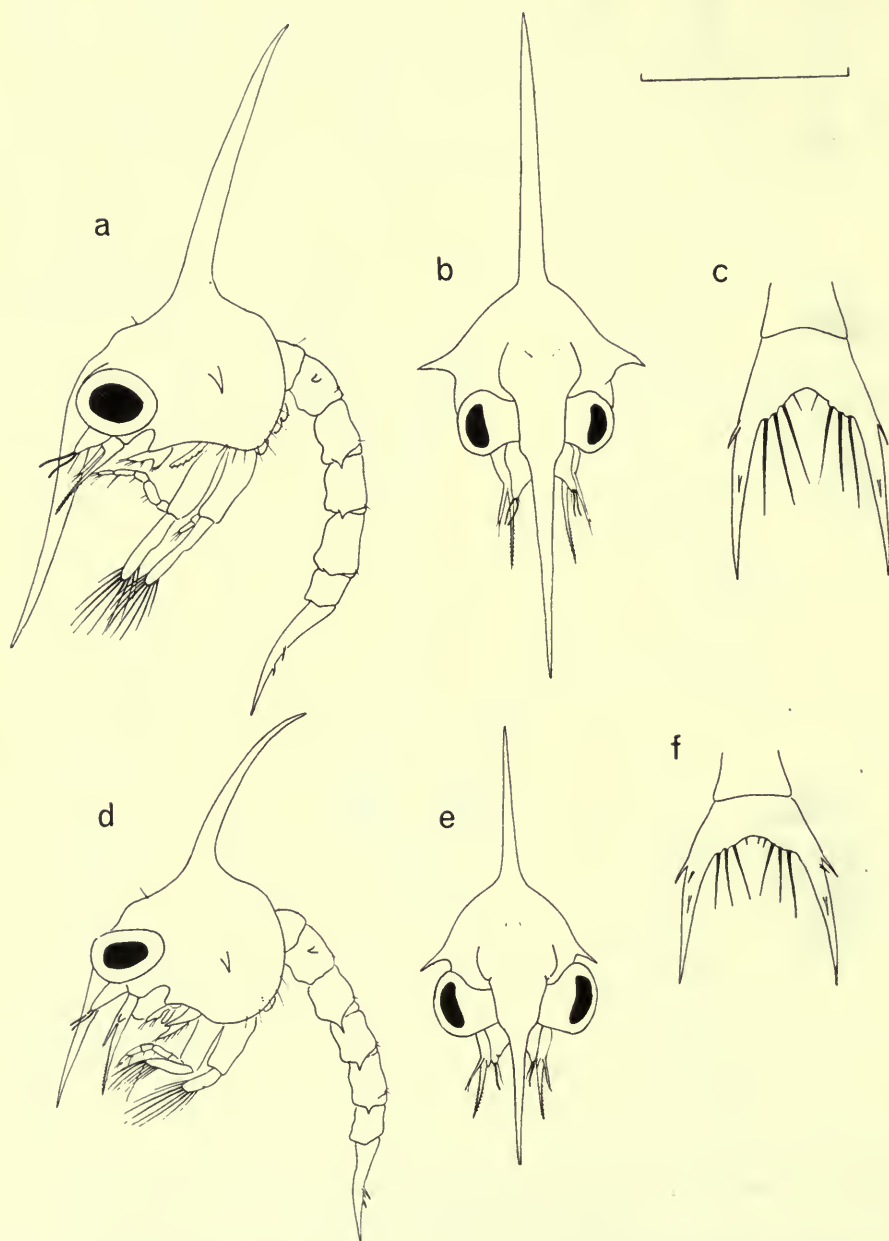


FIG. 5. Third zoea of *M. puber* (a, b and c) and of *M. holsatus* (d, e and f).
The bar scale represents 1.0 mm.

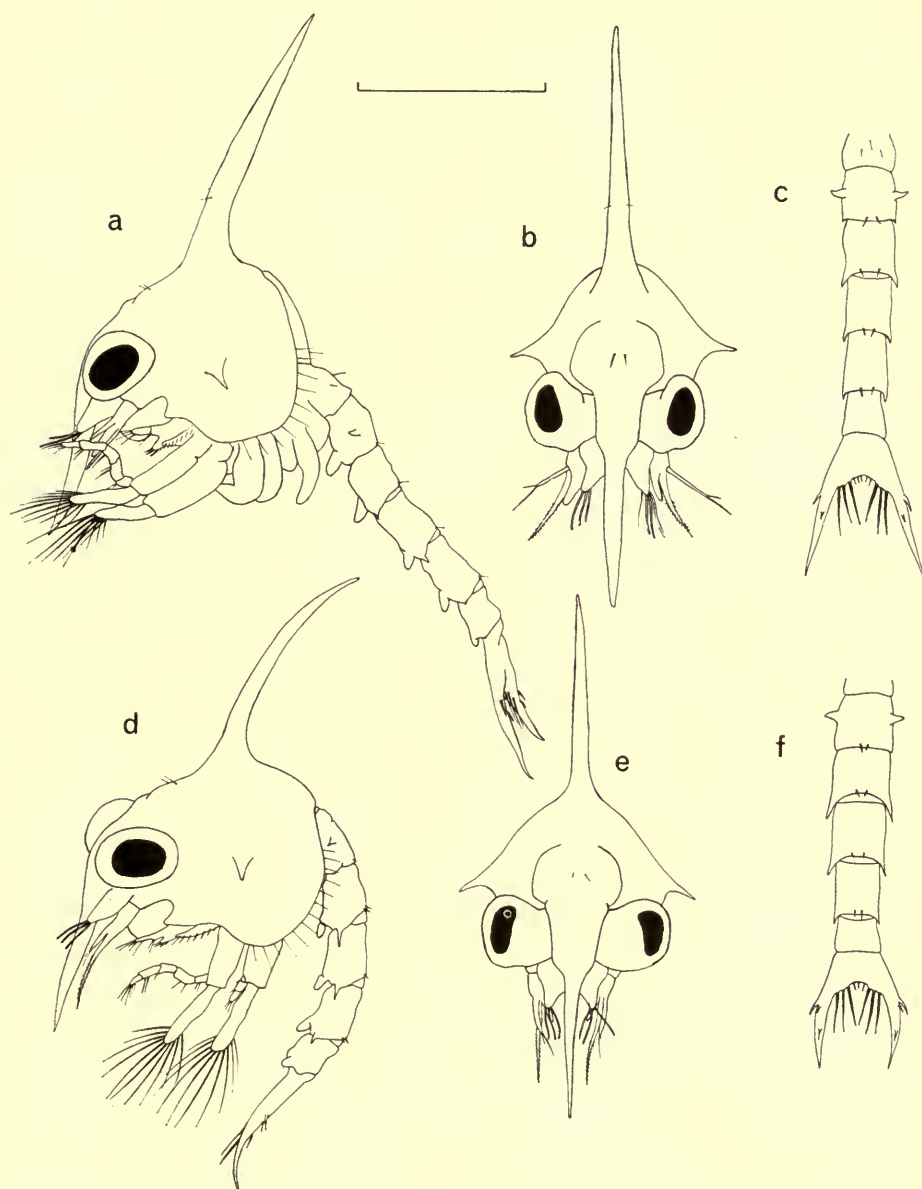


FIG. 6. Fourth zoea of *M. puber* (a, b and c) and of *M. holsatus* (d, e and f).
The bar scale represents 1.0 mm.

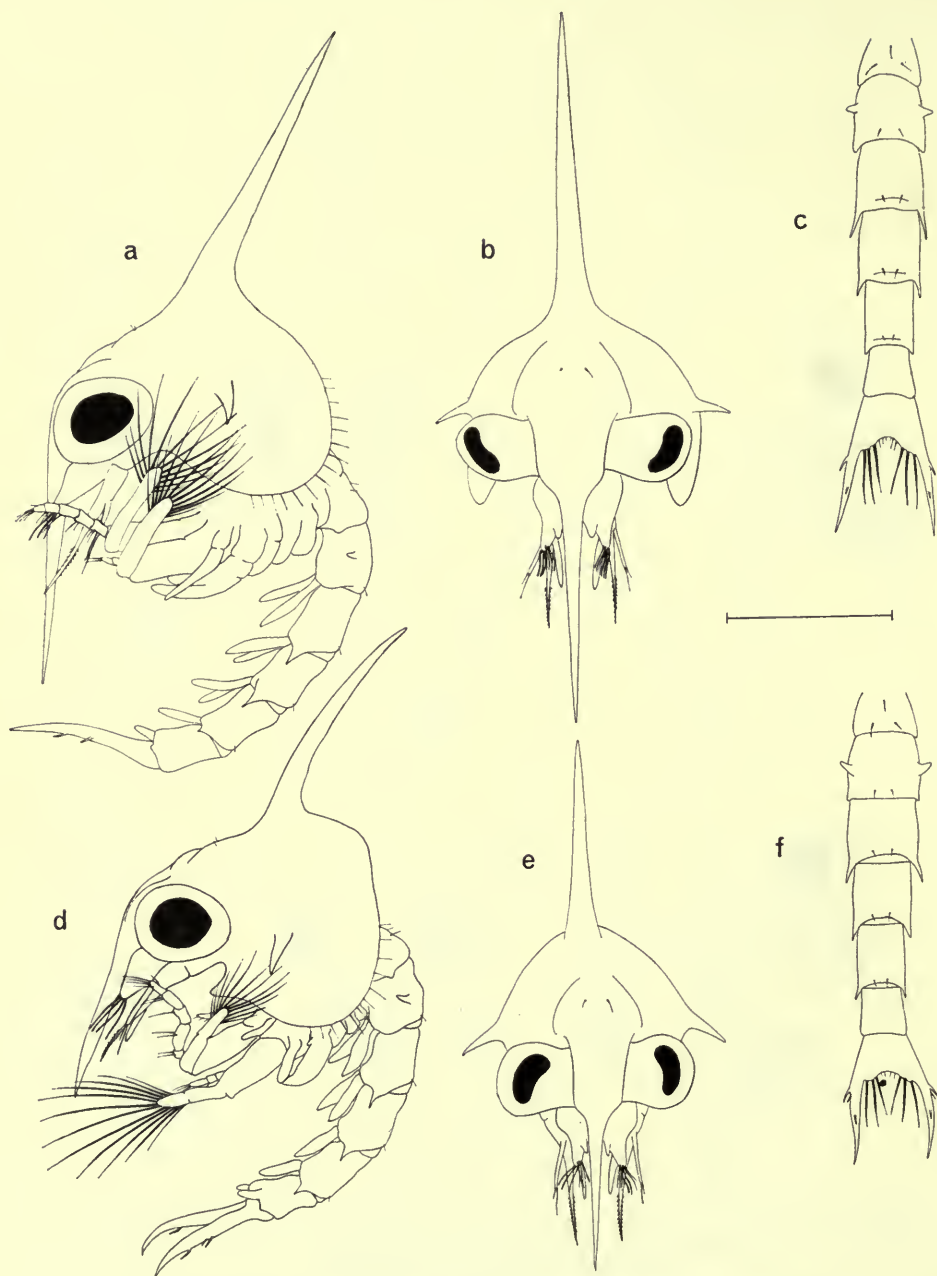


FIG. 7. Fifth zoea of *M. puber* (a, b and c) and of *M. holsatus* (d, e and f).
The bar scale represents 1.0 mm

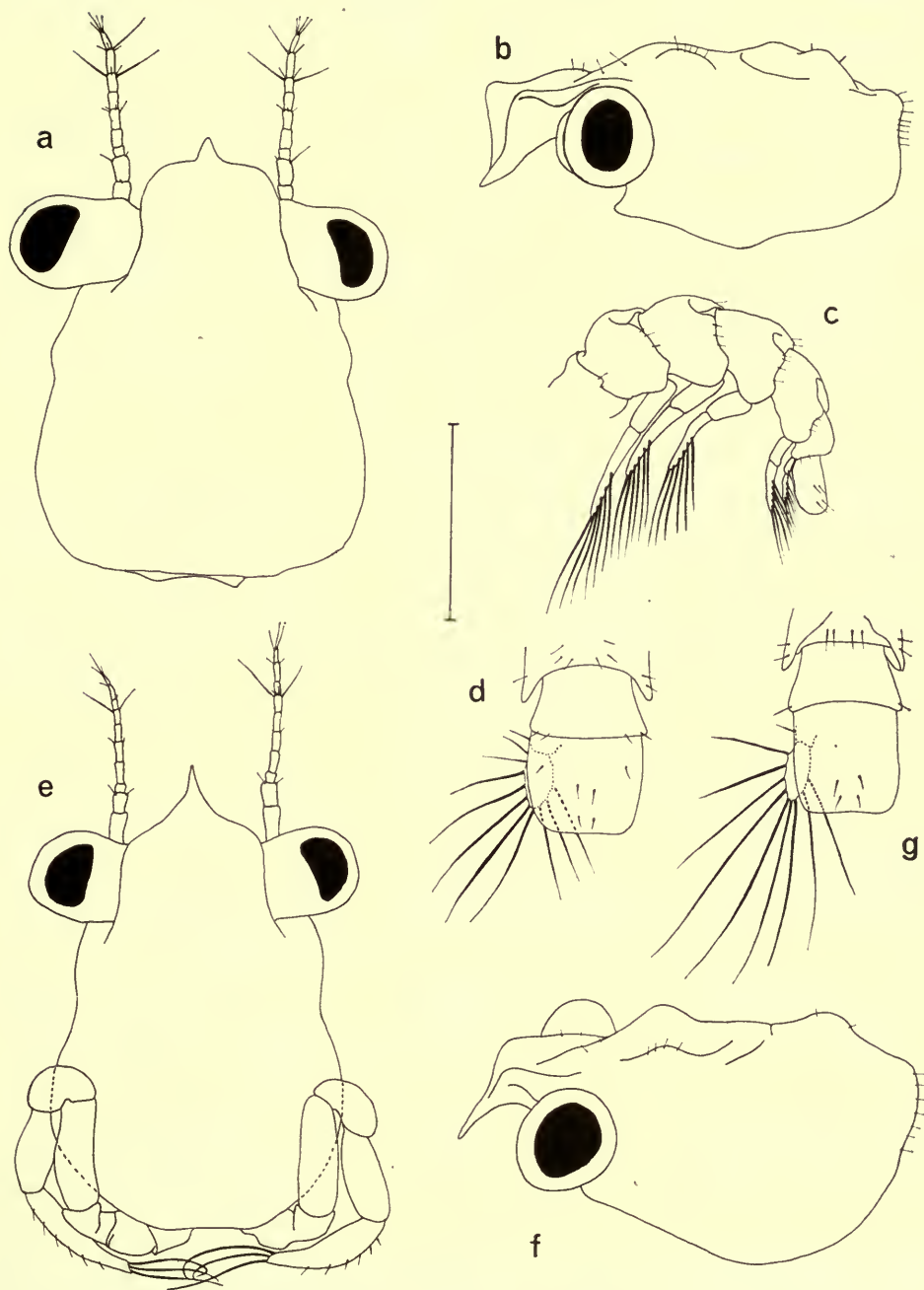


FIG. 8. Megalopa of *M. puber* (a-d) and of *M. holsatus* (e-g). The bar scales represent 0.5 mm for (d) and (g) and 1.0 mm for the remainder.

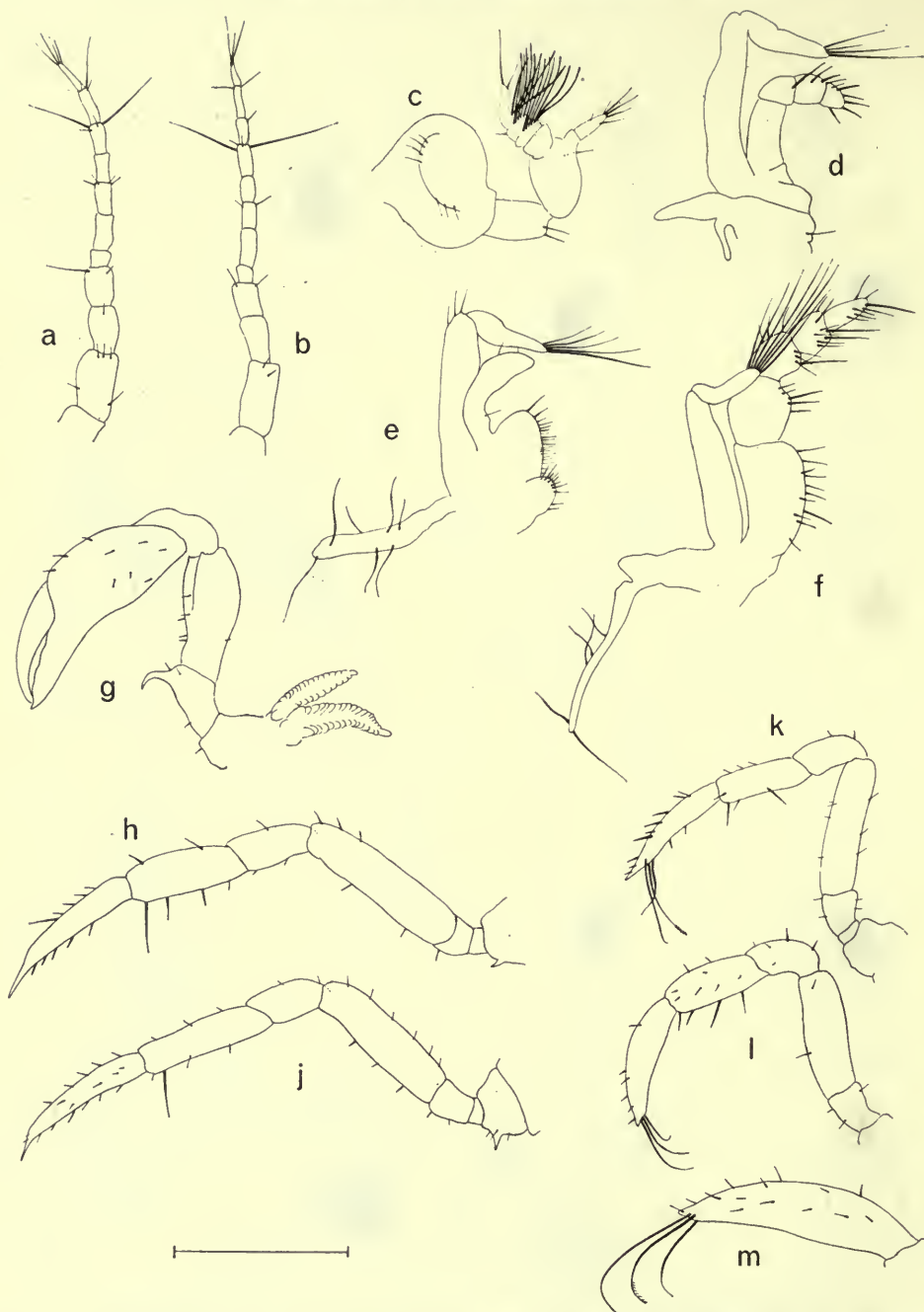


FIG. 9. Appendages of the megalopa stage in *M. puber* and *M. holsatus*: (a) antenna, *M. puber*; (b) antenna, *M. holsatus*; (c) antennule, *M. puber*; (d, e and f) first, second and third maxillipeds, *M. puber*; (g) cheliped, *M. holsatus*; (h, j) second and fourth pereopods, *M. puber*; (k) fifth pereopod, *M. puber*; (l and m) fifth pereopod, *M. holsatus*. The bar scale represents 0.5 mm for a-f and m, and 1.0 mm for g-l.

TABLE I

A comparison of the first zoeal stage in *Macropipus puber*, *M. holsatus* and *M. marmoreus**

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i> *
SIZE		
Carapace length :		
0.7 mm	0.4-0.6 mm	0.4 mm
Tip of dorsal to tip of rostral spines (a) :		
1.9-2.2 mm	1.1-1.3 mm	1.1 mm (1.18-1.24 mm†)
Width including lateral spines (b) :		
0.67-0.78 mm	0.61-0.74 mm	— (0.58-0.67 mm†)
Ratio a/b :		
2.68-2.80	1.80	— (1.84-2.0 mm†)
Length of dorsal spine :		
0.9 mm	0.4-0.5 mm	0.5 mm
CEPHALOTHORAX		
<i>Carapace</i> : Dorsal spine stout, straight or slightly curved at tip, much longer than carapace. Rostral spine straight or slightly curved anteriorly, longer than carapace. Lateral spines well developed. Carapace dorsal surface minutely rugose. Eyes sessile (Fig. 2a, b)	Dorsal spine slender, strongly curved posteriorly and equal to or only slightly longer than carapace. Rostral spine straight or curved backwards, equal to or shorter than carapace. Lateral spines well developed. Carapace smooth. Eyes sessile (Fig. 2d, e)	Similar to <i>holsatus</i>
<i>Antennule</i> : Unsegmented, with 2-3 terminal aesthetascs and 1-3 setae (Fig. 3a)	As <i>puber</i>	As <i>puber</i>
<i>Antenna</i> : Spinous process less than $\frac{3}{4}$ length of rostral spine. Exopod almost $\frac{1}{2}$ length of spinous process, with 2 unequal terminal setae (Fig. 3c)	Spinous process about as long as rostral spine. Otherwise as <i>puber</i>	Exopod with 3 terminal setae. Otherwise as <i>puber</i>
<i>Mandible</i> : without palp	As <i>puber</i>	As <i>puber</i>
<i>Maxillule</i> : Endopod with 5 or 6 setae on distal segment and 1 on proximal segment. Basal endite with 5 setae, coxal endite with 6 setae (Fig. 3j)	As <i>puber</i>	As <i>puber</i>
<i>Maxilla</i> : Endopod bilobed with 6-8 setae, basal endite with 6-8 setae, coxal endite with 7 setae. Scaphognathite with 5 setae, posterior one largest (Fig. 3k)	As <i>puber</i>	Scaphognathite with 6 setae ; otherwise as <i>puber</i>
<i>First maxilliped</i> : Basipodite with 10 setae (2, 2, 3, 3), 5-segmented endopod with 2, 2, 1, 2 and 5 setae, exopod with 4 natatory setae (Fig. 3l)	As <i>puber</i>	Basipodite with only 6 setae ; otherwise as <i>puber</i>

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i> *
<i>Second maxilliped</i> : Basipodite with 4 setae, 3-segmented endopod with 1, 1 and 4 or 5 setae, exopod with 4 natatory setae (Fig. 3 <i>m</i>)	As <i>puber</i>	As <i>puber</i>
<i>Pereiopods</i> : Limb buds just visible beneath carapace	Not visible	Not visible
ABDOMEN (Fig. 2 <i>c, f</i>)		
Five somites plus telson. Somites 2 and 3 with lateral processes, those of somite 3 minute	As <i>puber</i>	As <i>puber</i>
Somites 2-5 each with pair of minute dorsal setae and with postero-lateral margins with rounded expansions bearing small spinules	As <i>puber</i>	As <i>puber</i> , but postero-lateral expansions on somite 3 more prominent and acute
Telson with 2 lateral and 1 dorsal spines on each fork; posterior margin with 3 pairs of setae	As <i>puber</i>	As <i>puber</i>

* The data on *Macropipus marmoreus* in Tables 1-6 are taken from Goldstein, 1971.

† Figures from material deposited in the British Museum (Natural History).

TABLE 2

A comparison of the second zoeal stages in *Macropipus puber*, *M. holsatus* and *M. marmoreus*

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i>
SIZE		
Carapace length:		
0.85-0.90 mm	0.60-0.70 mm	0.60 mm
Tip of dorsal to tip of rostral spines (a):		
2.2-2.5 mm	1.40-1.60 mm	1.40 mm
Width including lateral spines (b):		
0.77-0.84 mm	0.71-0.76	-
Ratio a/b:		
2.85-3.01	1.87-2.15	-
Length of dorsal spine:		
c 1.0 mm	0.50-0.60 mm	0.50 mm
CEPHALOTHORAX		
<i>Carapace</i> : As in stage I but eyes now stalked (Fig. 4 <i>a, b</i>)	Similar to stage I but dorsal spine less than carapace length and eyes stalked (Fig. 4 <i>d, e</i>)	As <i>holsatus</i>
<i>Antennule</i> : 4-6 aesthetascs and 1-3 setae	As <i>puber</i>	As <i>puber</i>
<i>Antenna</i> : Endopod present as a bud. Spinous process < $\frac{1}{2}$ length of rostral spine. Exopod with 2 terminal setae (Fig. 3 <i>d</i>)	As <i>puber</i> , but spinous process almost as long as rostral spine	As <i>puber</i> , but exopod with 3 terminal setae

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i>
<i>Mandible</i> : As in stage I	As <i>puber</i>	As <i>puber</i>
<i>Maxillule</i> : Endopod as in stage I.	As <i>puber</i>	As <i>puber</i>
Endites with additional setae.		
Exopod seta present		
<i>Maxilla</i> : Endopod as in stage I.	As <i>puber</i>	As <i>puber</i>
Endites with additional setae.		
Scaphognathite with 11 setae, posterior one no longer significantly different		
<i>First maxilliped</i> : Exopod with 6 natatory setae ; otherwise as in stage I	As <i>puber</i>	Basipodite with 8 setae ; otherwise as <i>puber</i>
<i>Second maxilliped</i> : Endopod terminal segment with 4 setae.	As <i>puber</i>	Endopod terminal segment with 5 setae. Otherwise as <i>puber</i>
Exopod with 6 natatory setae		As <i>holsatus</i>
<i>Pereiopods</i> : Limb buds prominent	Limb buds just visible	

ABDOMEN (Fig. 4c, f)

Lateral processes on somite 3 present	As <i>puber</i>	Absent
Postero-lateral processes of abdominal somites acute but not prominent	As <i>puber</i>	Postero-lateral processes of somites 2-4 more prominent
One lateral spine on telson fork very small or absent	All 3 spines on telson forks well developed	As <i>holsatus</i>
Posterior telson margin with 4 pairs of setae	As <i>puber</i>	As <i>puber</i>

TABLE 3

 A comparison of the third zoeal stages in *Macropipus puber*, *M. holsatus* and *M. marmoreus*

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i>
SIZE		
Carapace length :		
0.96-1.0 mm	0.80-0.85 mm	0.70 mm
Tip of dorsal to tip of rostral spine (a) :		
3.0-3.3 mm	1.90-2.20 mm	1.70 mm
Width including lateral spines (b) :		
1.00-1.04 mm	0.90-0.95 mm	-
Ratio a/b :		
2.95-3.17	2.10-2.34	-
Length of dorsal spine :		
1.40 mm	c 0.85 mm	0.70 mm
CEPHALOTHORAX		
<i>Carapace</i> : As in stage II (Fig. 5a, b)	As in stage II but dorsal spine now equal to or slightly greater than carapace length (Fig. 5d, e)	As <i>holsatus</i>

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i>
SIZE		
<i>Antennule</i> : As in stage II	As in stage II	As in stage II
<i>Antenna</i> : Endopod bud almost $\frac{1}{3}$ length of exopod. Spinous process c $\frac{1}{2}$ length of rostral spine. Exopod with 2 terminal aesthetascs (Fig. 3e)	As <i>puber</i> but spinous process $> \frac{2}{3}$ length of rostral spine	Endopod bud almost $\frac{1}{3}$ length of exopod. Exopod with 4 terminal setae. Otherwise as <i>holsatus</i>
<i>Maxillule</i> : Additional setae on endites. Otherwise as in stage II	As <i>puber</i>	As <i>puber</i>
<i>Maxilla</i> : Scaphognathite with 13-14 setae	As <i>puber</i>	As <i>puber</i>
<i>First maxilliped</i> : Exopod with 8 natatory setae. Otherwise as in previous stages	As <i>puber</i>	As <i>puber</i>
<i>Second maxilliped</i> : Exopod with 8 natatory setae. Endopod terminal segment with 4 setae	Endopod with 3 terminal setae. Otherwise as <i>puber</i>	Endopod with 5 terminal setae. Otherwise as <i>puber</i>
ABDOMEN (Fig. 5c, f)		
Sixth somite separated from telson	As <i>puber</i>	As <i>puber</i>
Lateral processes of somite 3 now absent	As <i>puber</i>	As <i>puber</i>
Posterior-lateral processes of somites 3-5 less than $\frac{1}{4}$ length of succeeding somites	More prominent, those on somite 3 about $\frac{1}{3}$ length of somite 4	Similar to <i>holsatus</i>
Telson forks usually with only 2 spines; if third spine present it is minute	Telson forks each with 3 spines	As <i>holsatus</i>
Posterior telson margin with 4 pairs of setae	4 or 5 pairs of setae	5 pairs of setae

TABLE 4

A comparison of the fourth zoeal stages in *Macropipus puber*, *M. holsatus* and *M. marmoreus*

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i>
SIZE		
Carapace length :		
1.04-1.24 mm	1.10-1.20 mm	0.9 mm
Tip of dorsal to tip of rostral spine (a) :		
3.40-3.60 mm	2.60-2.90 mm	2.0 mm
Width including lateral spines (b) :		
c 1.20 mm	1.20-1.25 mm	—
Ratio a/b :		
2.86-2.96	2.10-2.29	—
Length of dorsal spine :		
1.30-1.40 mm	1.10-1.20 mm	0.90 mm

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i>
CEPHALOTHORAX		
<i>Carapace</i> : As in stage III (Fig. 6a, b)	As in stage III (Fig. 6d, e)	As in stage III
<i>Antennule</i> : 3 or 4 aesthetascs and 1 or 2 setae. Ventral flagellum may be present as small bud	As <i>puber</i> (Fig. o)	6 aesthetascs in two groups, plus a terminal seta
<i>Antenna</i> : Spinous process about $\frac{1}{2}$ length of rostral spine. Exopod $\frac{2}{3}$ length of spinous process, with 2 terminal setae. Endopod $\frac{1}{2}$ exopod (Fig. 3f)	Spinous process $> \frac{3}{4}$ length of rostral spine. Exopod $< \frac{1}{2}$ spinous process, with 2 terminal setae. Endopod $\frac{2}{3}$ exopod	Spinous process $\frac{1}{2}-\frac{2}{3}$ rostral spine. Exopod $< \frac{1}{2}$ spinous process, with 3 terminal setae. Endopod $< \frac{1}{2}$ exopod
<i>Maxillule</i> : Additional setae on endites. Otherwise as in previous stage	As <i>puber</i>	As <i>puber</i>
<i>Maxilla</i> : Scaphognathite with about 25 marginal setae	As <i>puber</i>	As <i>puber</i>
<i>First maxilliped</i> : Endopod segments with 2, 2, 1, 2 and 6 setae. Exopod with 10 natatory seta	As <i>puber</i>	As <i>puber</i>
<i>Second maxilliped</i> : 10 natatory setae. Otherwise as in stage III	10 natatory setae. Endopod with 4 terminal setae, i.e. as in <i>puber</i>	10 natatory setae. Endopod with 5 terminal setae
<i>Pereiopods</i> : First leg now clearly chelate	As <i>puber</i>	As <i>puber</i>
ABDOMEN (Fig. 6c, f)		
Postero-lateral processes of somites 3-5 longer than in stage III, those of somite 3 about $\frac{1}{4}$ length of somite 4	More prominent than in <i>puber</i> , those of somite 3 about $\frac{1}{3}$ somite 4	More prominent than in <i>holsatus</i> , those of somite 3 $> \frac{1}{2}$ somite 4
Telson forks each with 2 spines	3 spines	3 spines
Posterior margin with 10 or 11 setae	Posterior margin with 9 or 10 setae	Posterior margin with 10 setae
Pleopods and uropods present as buds	As <i>puber</i>	As <i>puber</i>

TABLE 5

A comparison of the fifth zoeal stages in *Macropipus puber*, *M. holsatus* and *M. marmoreus*

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i>
Size		
Carapace length :		
1.50-1.60 mm	1.30-1.48 mm	1.50 mm
Tip of dorsal to tip of rostral spine (a) :		
3.8-4.1 mm	3.00-3.50 mm	3.70 mm
Width including lateral spines (b) :		
1.60-1.70 mm	1.50-1.60 mm	—
Ratio a/b :		
2.4-2.5	2.0-2.2	—

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i>
SIZE		
Length of dorsal spine : 1.60-1.70 mm	1.3 mm	1.40 mm
CEPHALOTHORAX		
<i>Carapace</i> : As in previous stages (Fig. 7a, b)	As in previous stages (Fig. 7d, e)	As in previous stages
<i>Antennule</i> : 8-10 aesthetascs in 2 or 3 groups, plus a terminal seta.	As <i>puber</i>	13 aesthetascs plus terminal seta. Ventral flagellum well developed
Ventral flagellum well developed (Fig. 3b)		
<i>Antenna</i> : Spinous process about $\frac{1}{2}$ length of rostral spine. Exopod about $\frac{1}{2}$ length of spinous process ; 2 terminal setae. Endopod > exopod (Fig. 3g)	Spinous process > $\frac{3}{4}$ length of rostral spine. Otherwise as <i>puber</i>	Spinous process < $\frac{3}{4}$ rostral spine. Exopod < $\frac{1}{2}$ spinous process ; 4 terminal setae. Endopod > exopod
<i>Mandible</i> : Palp now present	As <i>puber</i>	As <i>puber</i>
<i>Maxillule</i> : Similar to stage IV	As <i>puber</i>	As <i>puber</i>
<i>Maxilla</i> : Schaphognathite with 30-36 marginal setae	As <i>puber</i>	Scaphognathite with about 40 setae
<i>First maxilliped</i> : As in stage IV but with 12 natatory setae (Fig. 3n)	As <i>puber</i>	As <i>puber</i>
<i>Second maxilliped</i> : Endopod terminal segment with 5 setae. Exopod with 12 natatory setae (Fig. 3o)	Endopod terminal segment with 4 or 5 setae. Exopod with 12 natatory setae	As <i>puber</i>
<i>Third maxilliped</i> : Well developed, biramous but unarmed	As <i>puber</i>	As <i>puber</i>
<i>Pereiopods</i> : Limbs clearly segmented	As <i>puber</i>	As <i>puber</i> ?
ABDOMEN (Fig. 7c, f)		
Postero-lateral processes of somites 3 and 4 about $\frac{1}{2}$ length of succeeding somites	As <i>puber</i>	Postero-lateral process of somite 3 > $\frac{1}{2}$ length of somite 4
Telson forks with 2 spines	3 spines	3 spines
Posterior margin with 10 or, more usually, 12 setae	10 setae	10 setae
Pleopods as long as succeeding somites	As <i>puber</i>	As <i>puber</i>

TABLE 6

A comparison of the megalopa stage in *Macropipus puber*, *M. holsatus* and *M. marmoreus*

<i>M. puber</i>	<i>M. holsatus</i>	<i>M. marmoreus</i>
SIZE		
Carapace length (a) : 1.66-2.09 mm	1.86-2.16 mm	c 2.0 mm
Carapace width (b) : 1.57-1.76 mm	-	1.65 mm
Ratio a/b : 1.12-1.26	c 1.40	c 1.22

M. puber
M. holsatus
M. marmoreus

CEPHALOTHORAX

Carapace : Relatively broad (see length/width ratio above). Rostrum directed ventrally and not prominent in dorsal view. Dorsal surface with two medial tubercles and two pairs of lateral ones. These tubercles, and particularly the posterior medial one, vary considerably in prominence. Front about $\frac{1}{2}$ maximum carapace width. Posterior margin almost straight and meeting lateral margins in abrupt angles (Fig. 8a, b)

Antennule : Three-segmented peduncle. Dorsal flagellum of 4 segments with 2 terminal setae and 3 groups of aesthetascs (Fig. 9c)

Antenna : Peduncle of 3 segments and flagellum of 7 segments, the fifth bearing 2 long setae (Fig. 9a)

Mandible : Well-developed 2-segmented palp with 8-10 setae

Maxillule : Endopod of 2 segments carrying 2 and 4 setae respectively. Endites with many marginal spines and setae

Maxilla : Endopod unarmed or with a single seta. Schaphognathite with about 50 marginal setae

First maxilliped : Exopod with 3-5 setae on the proximal segment and 4 or 5 on the distal one. Endopod unsegmented and reduced. Well-developed epipod of fairly constant width throughout its length (Fig. 9d)

Second maxilliped : Exopod 2-segmented, proximal with 1 small seta, distal with 4 or 5 terminal setae. Endopod 4-segmented, proximal naked. Epipod small (Fig. 9e)

Third maxilliped. Exopod with 6 terminal setae. Endopod of 5 segments, all armed. Epipod long (Fig. 9f)

Pereiopods. Cheliped with prominent curved spine on ischio-basis. Pereiopods 2-4 with straight spines on coxae (Fig. 9g, h, j)

Relatively narrow. Rostrum generally directed more anteriorly than in *puber* and therefore more prominent in dorsal view. Posterior margin arched and not meeting the lateral margins in abrupt angles. Otherwise as *puber* (Fig. 8e, f)

As *puber*

Flagellum of 8 segments (Fig. 9b)

As *puber*

As *puber*

As *puber*

As *puber*

As *puber*

As *puber*

Pereiopods 1-4 as in *puber*

Relatively broad. Rostrum prominent in dorsal view. Posterior-lateral tubercles absent. Front about $\frac{1}{2}$ maximum carapace width

As *puber*

Flagellum of 6 segments, the long setae being on the third

As *puber*

As *puber*

As *puber*

Epipod expanded basally. Otherwise as *puber*

As *puber*

As *puber*

Pereiopods 1-4 as in *puber*

*M. puber**M. holsatus**M. marmoreus*

CEPHALOTHORAX

Dactyl of pereopod 5 slender, length more than 5 times maximum width. Sensory setae clearly sub-terminal. Coxal spine minute or absent (Fig. 9*k*)

Dactyl of pereopod 5 broad, length about 4 times maximum width. Sensory setae virtually terminal (Fig. 9*l, m*)

As *holsatus*

ABDOMEN (Fig. 8*c*)

Somites 2-5 with postero-lateral expansions rounded

As *puber*

As *holsatus*

Exopods of pleopods on somites 2-5 with 17-19, 16-19, 17-18 and 13-15 setae respectively

Exopods of pleopods with 17-20, 19-20, 18-19 and 14-16 setae respectively

?

Endopods of pleopods with 3, or rarely 4, coupling hooks

As *puber*

As *puber*

Exopods of uropods with 8-10 setae
Telson usually narrows posteriorly, but may be almost square.

9 or 10 setae
Telson normally square, but may narrow posteriorly. Shape therefore not consistently distinguishable from *puber*

8 setae

?

Posterior margin usually straight or slightly concave, but may be markedly so

Telson dorsal surface with 2 pairs of postero-medial setae arranged in a rectangle elongated longitudinally. Additional pair of antero-lateral setae (Fig. 8*d*)

Telson dorsal surface with 2 pairs of postero-medial setae arranged in a rectangle elongated transversely. No antero-lateral setae (Fig. 8*g*)

Telson dorsal surface with 4 pairs of setae

Costlow and Bookhout mistakenly considered the species dealt with by Lebour (1928) under the name *Portunus* to belong to the sub-family Portuninae, so that with the exception of an inadequate account of the first zoeal stage of *Bathynectes longipes* Risso (Lebour, 1931) their description of the development of *Ovalipes ocellatus* seemed to be the first of a true polybiinid. Their discussion of possible sub-familial larval characters within the Portunidae was therefore largely invalid, but they nevertheless recognized the possession of sternal cornua in the megalopa stage as a portuninid character (see below). Roberts was similarly confused by the generic nomenclature when he compared his reared *Bathynectes* larvae with those of other species in the family and consequently did not recognize some larval differences which seem to be generic or even sub-familial.

On the other hand, Goldstein (1971) did not mix polybiinid and non-polybiinid species in her comparison with the larvae of *Macropipus marmoreus*, and was able to point out several differences between *M. marmoreus*, *Ovalipes ocellatus* and *Bathynectes superba*. The additional information presented here on the larvae of *M. puber* and *M. holsatus* now warrants a more detailed comparison in order to

establish the sort of generic distinctions which are likely to obtain between larval Polybiinae. The three genera *Macropipus*, *Ovalipes* and *Bathynectes* are therefore compared in Tables 7 and 8, revealing differences which at the moment appear to be generic.

TABLE 7

A comparison of the zoeal stages in *Macropipus*, *Bathynectes* and *Ovalipes*

	<i>Macropipus</i> *	<i>Bathynectes</i> †	<i>Ovalipes</i> ‡
ABDOMEN			
Dorso-lateral processes, somite 3	Stages I and II only	All stages	All stages
Dorso-lateral processes, somite 4	Absent	Absent	Present stages I-III
Dorso-lateral processes, somite 5	Absent	Absent	Present all stages
Postero-lateral processes, somite 4	< $\frac{1}{2}$ somite 5	> $\frac{1}{2}$ somite 5 from stage II	< $\frac{1}{2}$ somite 5
TELSON			
Telson fork armature, stage I	3 spines (1 dorsal)	3 spines (1 dorsal)	2 (both lateral)
Telson fork armature, stages II-V	2-3 (1 dorsal)	3 (1 dorsal)	2 (both lateral)
Anterior lateral telson spine	< $\frac{1}{4}$ fork length	> $\frac{1}{4}$ fork length	< $\frac{1}{4}$ fork length
Posterior margin, stage II	4 + 4 setae	3 + 3	3 + 3
Posterior margin, stage III	5 + 5 setae	4 + 4	4 + 4
FIRST MAXILLIPED			
Basipodite medial setae	6-10	10	4-?
Endopod terminal setae, stage III	5	6	6
Natatory setae, stages II-V	6, 8, 10, 12	6, 8, 10, 12	7, 8, 10, 14
SECOND MAXILLIPED			
Natatory setae, stages II-V	6, 8, 10, 12	6, 8, 10, 12	7, 10, 12, 15

* Based on *Macropipus puber* and *M. holsatus* described in this paper, and on *M. marmoreus* described by Goldstein, 1971.

† Based on *Bathynectes superba* described by Roberts, 1969.

‡ Based on *Ovalipes ocellatus* described by Costlow and Bookhout, 1966.

TABLE 8

A comparison of the megalopa stage in *Macropipus* and *Ovalipes*

	<i>Macropipus</i> spp.	<i>Ovalipes ocellatus</i> *	<i>Ovalipes punctatus</i> †
Lateral knobs on carapace	Absent	Present	Absent
Rostral spine	Directed downwards‡	Directed forwards	Directed forwards
Coxal spines on legs 2-4	Present	Absent	Absent
Maxillule endopod, basal segment	2 setae	3 setae	2 setae
Maxilla endopod	Unarmed or with a single seta	7 setae	6 setae
Maxilliped 1, endopod	Unsegmented, expanded at tip with 3-6 setae	Segmented, not expanded, about 17 setae	Unsegmented, with about 17 setae
Dactyl, pereopod 5	Not markedly flattened ; L : W > 4 : 1	Markedly flattened ; L : W < 3.5 : 1	As <i>O. ocellatus</i>
Abdominal somite 5, postero-lateral margins	Rounded	?	Acute
Pleopods, endopods	3-4 hooks	?	7 hooks
Pleopods, exopods	13-20 marginal setae	?	31-40 marginal setae
Uropods, proximal segment	0-1 seta	?	3 setae
Uropods, distal segment	8-10 marginal setae	?	About 22 marginal setae

* Data from Costlow and Bookhout, 1966.

† Data from Muraoka, 1969.

‡ Except *depurator* according to Lebour (1928).

In the zoeal phase *Ovalipes* can be distinguished from the other two genera by the possession of dorso-lateral processes on the fifth abdominal somite in all stages and on the fourth somite up to stage III, and in lacking a dorsal spine on the telson forks. *Macropipus* differs from both *Ovalipes* and *Bathynectes* in losing the dorso-lateral process on the third abdominal somite after the second stage, while in all the zoeal stages *Bathynectes* has much longer postero-lateral processes on the fourth somite and also a much more prominent anterior spine on the telson fork than either *Macropipus* or *Ovalipes*.

Unfortunately Roberts was unable to obtain the megalopa of *Bathynectes* so that in this stage *Macropipus* can be compared only with *Ovalipes*, and even here much of the information which would be useful in such a comparison is not available (see Table 8). Nevertheless, the megalopae of *Ovalipes* seem to differ from all described *Macropipus* megalopae in having more setose appendages, particularly the abdominal ones, and in lacking the prominent spines on the coxal segments of legs 2, 3 and 4.

Possible sub-familial characters of the Polybiinae can be discussed only in relation to the Carcininae and the Portuninae, for which at least some larval information has been obtained. Within the Carcininae, although Couch hatched and described the

first zoea of the common and widely distributed shore crab, *Carcinus maenas* (L.), as early as 1844 and there were many subsequent accounts of some or all of the larval stages of this species, they have only recently been described in detail from reared material and compared with the closely related *C. mediterraneus* Czerniavsky (see Rice and Ingle, 1975). The only other carcininid genus of which larvae are known is *Portumnus*, Lebour (1944a) having hatched and reared the first two stages of *P. latipes* and attributed to the same species a plankton-caught terminal zoea which moulted to the megalopa and then to the first crab stage in the laboratory. Another plankton-caught megalopa which moulted to a first crab had been ascribed to *Xavia biguttata* (Risso) (as *Portumnus biguttatus*) in an earlier paper (Lebour, 1928); these two megalopae were very distinct.

There are many morphological details, particularly in the setation of the appendages, in which the larvae of *Carcinus* and *Portumnus* differ from those of the polybiinid species discussed above. Some of these features may be good sub-familial characters, but in addition there are a number of much more obvious differences which appear to enable larval carcininids to be distinguished readily from polybiinids. Firstly, the two *Carcinus* species, and probably also *Portumnus*, pass through only four zoeal stages, whereas all the known polybiinids have five zoeae. The consequent differences in developmental rates result in distinct combinations of characters in the two sub-families; pleopod buds, for instance, occur on zoeae with 8 natatory setae on the exopods of the maxillipeds in the Carcininae, that is in the third stage, whereas the pleopods do not appear in the Polybiinae until the fourth zoeae in which the maxillipeds carry 10 setae. This character would not, of course, enable stage I and II carcininid and polybiinid larvae to be separated, but the zoeae of *Carcinus* and *Portumnus* differ from those of *Macropipus* in these early stages, and from those of *Bathynectes* and *Ovalipes* at all stages, in having no dorso-lateral processes on the third abdominal somite. Carcininid zoeae also differ from the polybiinids, certainly from the third stage, in having only three pairs of setae on the posterior margin of the telson, whereas all the known larval *Macropipus*, *Bathynectes* and *Ovalipes* add at least one extra pair of setae and often more. But the most obvious carcininid zoeal character, which distinguishes them from all other known portunids, both polybiinids and portuninids (see below), is the total absence of lateral carapace spines.

In the megalopa stage *Carcinus* and *Portumnus* differ from *Macropipus* in having no coxal spines on pereopods 2-4, and from *Ovalipes* in having rounded posterior-lateral margins to the fifth abdominal somite. Both polybiinid genera differ from *Carcinus* in having more setae on the pleopods and uropods, the difference being more marked in *Ovalipes* than in *Macropipus*.

In terms of the number of species of which larvae have been described, the Portuninae is the best known sub-family of swimming crabs. However, although there are published accounts of one or more stages of five portuninid genera, many of these accounts are inadequate, several are based on material collected from the plankton and therefore of doubtful identity and, of the reared species, the complete development is known for only four (see Table 9). Nevertheless, the available data do allow some general comments about portuninid larvae to be made.

TABLE 9

Descriptions of larval Portuninae referred to in the accompanying discussion*

SPECIES	STAGE(S)	SOURCE OF MATERIAL	AUTHOR
<i>Callinectes sapidus</i>	Zoeae I-VII, megalopa	Hatched and reared	Costlow and Bookhout, 1959
<i>Scylla serrata</i>	Zoeae I-V, megalopa	Hatched and reared	Ong, Kah Sin, 1964
<i>Scylla serrata</i>	Zoea I	Hatched	Naidu, 1955
<i>Charybdis acuta</i>	Zoeae I-VI, megalopa	Hatched and reared	Kurata and Omi, 1969
<i>Charybdis japonica</i>	Zoeae I-VI, megalopa	Hatched and reared	Yatsuzuka, 1952
<i>Charybdis lucifera</i>	Zoea I	Hatched	Hashmi, 1970
<i>Charybdis annulata</i>	Zoea I	Hatched	Hashmi, 1970
<i>Charybdis callianassa</i>	Zoea I	Hatched	Hashmi, 1970
<i>Charybdis orientalis</i>	Zoea I	Hatched	Hashmi, 1970
<i>Charybdis 6-dentata</i>	Zoea I	Plankton	Aikawa, 1937
<i>Charybdis bimaculata</i>	Zoea IV, megalopa	Plankton	Aikawa, 1937
<i>Portunus trituberculatus</i>	Zoea I	Hatched	Aikawa, 1937
<i>Portunus pelagicus</i>	Zoea I, megalopa	Plankton	Aikawa, 1937
<i>Portunus pelagicus</i>	Zoea I	Hatched	Delsman and De Man, 1925
<i>Portunus pelagicus</i>	Zoeae I-IV, megalopa	Hatched and reared	Yatsuzuka, 1962
<i>Portunus pelagicus</i>	Zoeae I, II and III ?	Hatched and plankton	Prasad and Tampi, 1953
<i>Portunus sayi</i>	Zoea I ?	Plankton	Lebour, 1944b
<i>Portunus depressifrons</i>	Zoea I ?	Plankton	Lebour, 1944b
<i>Thalamita crenata</i>	Zoea I	Hatched	Prasad and Tampi, 1953
<i>Thalamita sima</i>	Megalopa	Plankton	Muraoka, 1969
<i>Portunus sanguinolentus</i>	Zoea I	Plankton	Chhapgar, 1956
<i>Portunus pelagicus</i>	Zoea I	Plankton	Chhapgar, 1956
<i>Charybdis orientalis</i>	Zoea I	Plankton	Chhapgar, 1956
<i>Thalamita crenata</i>	Zoea I	Plankton	Chhapgar, 1956

* The list is by no means complete, a number of publications having been omitted because the identifications are particularly unreliable, the descriptions are inadequate or they have been superseded by subsequent work. A more serious omission, however, is the excellent account of the larval development of *Portunus spinicarpus* by Bookhout & Costlow (1974), which was not seen until after this manuscript had been submitted. Fortunately, *P. spinicarpus* is a typical portuninid and its omission does not affect the discussion of sub-familial larval characters in this paper.

Firstly, there is considerably more variation in the rate of development in the portuninids than in either the polybiinids or carcininids, the number of zoeal stages ranging from seven in *Callinectes sapidus* through six in *Charybdis acuta* and *C. japonicus*, five in *Scylla serrata*, to four in *Portunus pelagicus* (or even three, according to Prasad and Tampi, 1953, although the sizes given for their zoeae indicate that they may have missed at least one stage). This heterogeneity extends also to some morphological features, such as the telson fork armature, for while there is a tendency to a reduction of the number of spines on the telson forks in the later stages of portuninids, just as in the other two sub-families, there is considerable variation even in the first

zoeal stage. Thus while some species (e.g. *Scylla serrata*, *Portunus depressifrons* and *P. sayi*) retain all three spines on each fork, one of the lateral spines is reduced to a fine hair in *Charybdis callianassa*, *C. lucifer* and *C. annulata*, and totally disappears in *Portunus trituberculatus*, *P. pelagicus*, *P. sanguinolentus*, *Callinectes sapidus*, *Charybdis japonicus*, *C. 6-dentata*, *C. orientalis* and *Thalamita crenata*. Finally, Chhapgar (1956) illustrates only a single spine on the telson forks of his larvae of *Charybdis orientalis*, *Thalamita crenata*, *Portunus sanguinolentus* and *P. pelagicus*.

This variability allows the zoeae of individual portuninid species to be distinguished fairly easily from all known polybiinids, but there does not seem to be a single feature which will separate the two sub-families at all zoeal stages. For those characters which are common to all portuninid zoeae, such as the possession of well-developed dorsal, rostral and lateral carapace spines, dorso-lateral processes on abdominal somites 2 and 3, postero-lateral processes on somites 3-5 in the later stages, telson forks usually with at least two spines of which one is dorsal, and the addition of at least one extra pair of setae on the posterior margin of the telson from stage II, are almost without exception shared also with some or all of the polybiinids. In fact, the only feature we have noticed which seems to be unique to portuninid zoeae is the absence of any setae on the middle segment of the endopod of the first maxilliped in the first zoeal stage.* [Hashmi (1970) figures a seta in this position in the first zoea of *Charybdis callianassa*, but we have been unable to confirm its existence in material deposited by him in the collections of the British Museum (Natural History).] Even this fine distinction disappears in the later stages of *Scylla serrata* and *Charybdis acuta*, and as early as the second zoea in *Callinectes sapidus*, and would hardly seem sufficient to support the sub-familial separation of the Portuninae and Polybiinae based on adult characters. But in the megalopa stage there are much clearer distinctions between the Portuninae, on the one hand, and all other described swimming crabs, on the other. All portuninid megalopae, for instance, have prominent postero-lateral spines on the fifth abdominal somite which are found only in *Ovalipes punctatus* amongst the Carcininae and Polybiinae. Similarly, there is a tendency in the Portuninae to increase the number of setae on the uropods beyond that found in the other two families, again with the exception of *Ovalipes*, but since this armature ranges in *Portunus pelagicus* from 10 or 11 (according to Aikawa, 1937, and Yatsuzuka, 1962) to 20 (according to Prasad and Tampi, 1953) the reliability of this character is very doubtful. By far the most striking portuninid megalopal character, however, is the possession of a pair of prominent postero-ventrally directed spines, the so-called sternal cornua, arising from the sternum between the last pair of legs. This feature at once distinguishes the portuninids, not only from the carcininids and polybiinids, including *Ovalipes*, but also from all other brachyuran megalopae so far described.

These differences between the larvae of the Carcininae, the Polybiinae and the Portuninae are summarized in the following diagnoses.

* One other possibly unique portuninid zoeal character is the position of the pair of fine setae on the dorsal surface of the carapace. In the Carcininae and Polybiinae these setae are anterior to the dorsal spine and close together, whereas in the Portuninae they are between the dorsal and lateral carapace spines. However, they may not always be present, for Costlow and Bookhout, 1959, specifically looked for them in *Callinectes* and failed to detect them.

Carcininae

ZOEAE

Four zoeal stages ; carapace without lateral spines ; dorso-lateral projections on abdominal somite 2 only ; postero-lateral processes of abdominal somites 3 and 4 less than half length of succeeding somites in all stages ; telson fork armature reduced to a single spine in late stages ; telson posterior margin with 3 + 3 setae in all stages ; middle segment of endopod of first maxilliped armed with a single seta in stage I.

MEGALOPA

Rostrum directed forwards or downwards ; no coxal spines on pereopods ; no sternal cornua ; pleopods with 9-12 (rarely 13) marginal setae ; uropods with 4-10 marginal setae ; postero-lateral spines on abdominal somite 5 absent.

Polybiinae

ZOEAE

Five zoeal stages ; well-developed lateral carapace spines ; dorso-lateral projections on abdominal somites 2 and 3, at least in the early stages ; postero-lateral processes of abdominal somites 3 and 4 usually less than half length of succeeding somites in later stages ; telson forks with at least 2 spines in all stages ; telson posterior margin with at least 4 + 4 setae in late stages ; middle segment of endopod of first maxilliped armed in stage I.

MEGALOPA

Rostrum directed forwards or downwards ; coxal spines on pereopods 2-4 present (*Macropipus*) or absent (*Ovalipes*) ; no sternal cornua ; pleopods with 14-20 (rarely 13) marginal setae (*Macropipus*) or 31-40 (*Ovalipes*) ; uropods with 8-10 marginal setae (*Macropipus*) or c 22 (*Ovalipes*) ; postero-lateral spines on abdominal somite 5 absent (*Macropipus*) or present (*Ovalipes*).

Portuninae

ZOEAE

Four to seven zoeal stages ; well-developed lateral carapace spines ; dorso-lateral projections on abdominal somites 2 and 3 in all stages ; postero-lateral processes of abdominal somites 3 and 4 more than half length of succeeding segments in late stages ; telson forks with at least 2 spines in all stages (except according to Chhappar) ; telson posterior margin with at least 5 + 5 setae in late stages ; middle segment of endopod of first maxilliped unarmed in stage I.

MEGALOPA

Rostrum directed forwards ; coxal spines absent from pereopods 3 and 4 but may be present on pereopod 2 (*Charybdis* and *Scylla*) ; sternal cornua always present ;

pleopods with 17-26 marginal setae ; uropods with 11-14 marginal setae ; posterio-lateral spines of abdominal somite 5 always prominent and usually over-reaching somite 6.

THE BEARING OF LARVAL CHARACTERS ON PORTUNID CLASSIFICATION

The above distinctions between the larval stages of the Carcininae, Polybiinae and Portuninae generally support the current divisions within the family which are based largely on the degree to which the adults show adaptations to the swimming habit. These adaptations include a tendency to lighten the integument, to flatten the carapace and extend it laterally to improve the dynamics of sideways swimming, to change the orientation of the leg articulations and to flatten the limbs and fringe them with setae to produce effective paddles (Hartnoll, 1971). There is a good deal of variation in the extent of these adaptations within the sub-families, but in general the Carcininae and Portuninae represent the extreme conditions, the Carcininae showing the least and the Portuninae the most modification from the unspecialized brachyuran form. The Polybiinae are somewhat intermediate between the other two sub-families and even within the genus *Macropipus* there is a considerable range in swimming adaptations, and particularly in the degree of flattening of the legs (see Palmer, 1927).

This situation is reflected in the larvae, for while the Carcininae and Portuninae exhibit major differences in both the zoea and megalopa stages, the Polybiinae have zoeae which resemble the Portuninae while the megalopae are more similar to those of the Carcininae. This does not, of course, necessarily mean that the Polybiinae stand phylogenetically between the Carcininae and the Portuninae, and the presence in the zoeae of *Ovalipes* of characters such as the dorso-lateral processes on abdominal somites 4 and 5, which are apparently unique amongst the portunids, indicates that this genus, at least, is well away from any such route.

It has been generally accepted that the swimming adaptations of adult portunids are secondary acquisitions and that the relative absence of such adaptations in the Carcininae is therefore a primitive condition. There have, however, been suggestions that the morphological series into which extant swimming crabs can be arranged might be read in the opposite direction, so that the loss of swimming adaptations becomes an advanced feature (Palmer, 1927; Lebour, 1928). The information available from the larval stages does not provide any clear evidence for one or other of these views. For the main character distinguishing carcininid larvae from all other portunids, that is the absence of lateral carapace spines in the zoeal stages, occurs sporadically in a number of other brachyuran families and does not seem to be of any particular phylogenetic importance. On the other hand, the presence of sternal horns on all portuninid megalopae, a feature which is unique not only amongst the Portunidae but also amongst the Brachyura generally, indicates that this sub-family probably represents the end of a portunid evolutionary line rather than an intermediate stage.

It is possible, of course, that the Polybiinae are phylogenetically more 'primitive' than either the Carcininae or the Portuninae, in the sense that they are closer to the

ancestral stock or stocks of both sub-families. This would require two parallel evolutionary tendencies within the Portunidae, one involving a loss of swimming adaptations and a return to the relatively unspecialized brachyuran condition of the Carcininae, and the other leading to the increased specialization of the Portuninae.

Morphological details of the larvae of more swimming crab species, and particularly those of the sub-families of which the larval stages are totally unknown at present, might help to clarify these relationships within the Portunidae and between the swimming crabs and other brachyuran families. But the pelagic larvae are generally much more similar than the adults since they show none of the specializations for such habits as swimming, burrowing or commensalism which characterize the benthic adult phase. A study of larval systematics will therefore probably require a numerical approach, making use of a much greater variety of features than has usually been used in the past. Such an investigation is underway at the moment using the available published information for all brachyuran larvae, and it is hoped that this will not only supplement the systematics based on adult characters but will also help in the identification of unknown plankton-caught larvae.

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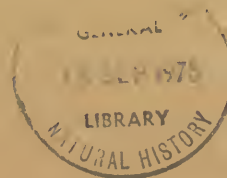
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STREPTAXIDAE (MOLLUSCA, GASTROPODA: PULMONATA) FROM ALDABRA ISLAND, WESTERN INDIAN OCEAN

By A. C. VAN BRUGGEN

INTRODUCTION

THE pulmonate gastropod family Streptaxidae has an almost circumtropical distribution. Species are particularly numerous and diverse on the African continent; in addition the family is well represented on Madagascar, the Comoros, Seychelles and Mascarene Islands in the Western Indian Ocean. Aldabra atoll ($9^{\circ}24' \text{ S } 46^{\circ}20' \text{ E}$) is situated in the southwestern Indian Ocean (fig. 5); the nearest land of any magnitude is the island of Madagascar at a distance of about 420 km to the southeast and the African mainland at about 640 km to the west. Apart from very small atolls the nearest high islands are the Comoros at a distance of about 400 km to the southwest. The Seychelles are further away than both the African continent and Madagascar, viz. about 1200 km to the northeast.

Maxwell Smith (1909) was the first to record the presence of streptaxids on the island of Aldabra. Messrs J. F. Peake and J. D. Taylor have been participating in various phases of the Royal Society Expedition to Aldabra. In the course of their work on the atoll and its satellite island Assumption they have collected extensive series of streptaxid shells, the study of which they have entrusted to the present author. Aldabra and Assumption appear to harbour four species of Streptaxidae, three of which are extinct. All are described below followed by a discussion on their relationships and possible derivation.

The following abbreviations have been used:

BMNH	British Museum (Natural History), London;
NM	Natal Museum, Pietermaritzburg;
PSTE/JCFF	Percy Sladen Trust Expedition, leg. J. C. F. Fryer;
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden;
RSE	Royal Society Expedition;
l/d	ratio length/major diameter of shells.

The l/d has been calculated from micrometer readings, so that these figures may not always agree with those calculated from the accompanying measurements in mm.

Acknowledgements are due to Mr J. F. Peake and Dr J. D. Taylor, and the staff of the Mollusca Section of the British Museum (Natural History) for assistance in various respects. I am also indebted to The Royal Society, who have fostered and encouraged research on Aldabra Island. Thanks are due to Dr A. Zilch of the Senckenberg-Museum, Frankfurt am Main, for hospitality for comparative studies at his institute, and to Mr R. N. Kilburn of the Natal Museum for lending the

material described by Connolly in 1925. The illustrations are due to the professional skill of H. Heijn, staff artist of the Department of Systematic Zoology of Leiden University.

Localities have been pinpointed by means of their coordinates on the Royal Society grid as shown on the map by Stoddart in Westoll & Stoddart (1971) (between pp. 632 and 633).

The fossils have been registered in the Mollusca Section, Department of Palaeontology, and recent specimens bear registration numbers of the Mollusca Section, Department of Zoology, both in the British Museum (Natural History).

Gulella gwendolinae (Preston, 1910)

Ennea gwendolinae Preston, 1910, *Ann. Mag. nat. Hist.* (8) **6**: 527, pl. 7, fig. 3 ('Shimbi Hills, British East Africa').

Gulella gwendolinae: Verdcourt, 1962, *Annls Mus. r. Afr. centr. Sér. 8° Sci. zool.* **106**: 8 ('K [= Kenya], Shimba Hills and nearby coastal forests').

Gulella gwendolinae aldabrae n. subsp.

Figs. 1, 6

Gulella gwendolinae: Connolly, 1925, *J. Conch., Lond.* **17**: 265 ('Aldabra I. '); Germain, 1934, 67me Congr. Soc. sav.: 131 (footnote, 'Aldabra').

Ennea gwendolinae: Barnacle, 1962, *J. Seych. Soc.* **2**: 54 ('Aldabra').

Ennea alauda Sykes (nomen nudum): Barnacle, 1962, *J. Seych. Soc.* **2**: 54 ('Ile Picard, Aldabra').

Ennea sp.: Smith, 1909, *Nautilus* **23**: 69 ('Grande Terre. Ile Picard. Iles Vertes').

DIAGNOSIS. A subspecies of *Gulella gwendolinae* in size and shape in between the typical form and *G. g. tsadiensis* Blume, but with the aperture smaller than in the other subspecies; dentition as in typical form, but with little variation.

DESCRIPTION OF SHELL. Shell (fig. 1) small, (sub)cylindrical, with open umbilicus, smooth, creamy white. Spire produced, sides subparallel, apex flattened, obtusely conical. Whorls six to seven, slightly convex, almost completely smooth, only with faint traces of costulation or striation below the sutures and around the umbilicus, initial whorls rarely with indication of spiral sculpture; sutures shallow, simple, somewhat impressed, (sub)crenellate. Aperture quadrate, rounded at base, peristome incrassate and reflected, white and glossy, with six-fold dentition: a reasonably well-developed oblique angular lamella touching the tip of the labrum; two subequal mid-labral denticles on a slightly raised common base, labral complex corresponding to shallow but extensive external pit; a mid-basal denticle, also corresponding to a little and shallow outside depression, which is sometimes hardly noticeable; bipartite columellar process consisting of two prominent subequal denticles on a raised common base – the bifurcation of the columellar process may vary in depth.

MEASUREMENTS OF SHELL: 3.6–5.1 × 1.4–1.9 mm, *l/d* 2.23–2.84 (mean 2.53, average of 56:2.56), length last whorl 1.8–2.4 mm, aperture length × width 1.1–1.6 × 1.0–1.4 mm, 6–7 whorls. Table 1 details the measurements of 56 adult shells; the holotype is no. 34.

TABLE I

Measurements of shells of *Gulella gwendolinae aldabrae* n. subsp. from Aldabra and Assumption

no.	length × maj. diam.	<i>l/d</i>	length last whorl	aperture length × width	number of whorls	locality
1	3.6 × 1.4 mm	2.48	1.8 mm	1.2 × 1.1 mm	6½	Anse Cedres
2	3.6 × 1.5 mm	2.35	1.8 mm	1.1 × 1.1 mm	6	Aldabra, Sykes
3	3.6 × 1.5 mm	2.37	1.9 mm	1.2 × 1.1 mm	6	Aldabra, Sykes
4	3.6 × 1.6 mm	2.28	1.9 mm	1.2 × 1.1 mm	6	Ile Michel
5	3.7 × 1.4 mm	2.68	1.8 mm	1.2 × 1.0 mm	6½	Aldabra, Thomasset
6	3.7 × 1.4 mm	2.61	1.9 mm	1.2 × 1.1 mm	6	Anse Cedres
7	3.7 × 1.4 mm	2.60	1.9 mm	1.2 × 1.1 mm	6½	Aldabra, Sykes
8	3.7 × 1.6 mm	2.40	1.9 mm	1.2 × 1.2 mm	6	Assumption, Sykes
9	3.8 × 1.5 mm	2.54	1.9 mm	1.2 × 1.1 mm	6½	Anse Cedres
10	3.8 × 1.6 mm	2.44	1.9 mm	1.2 × 1.1 mm	6¼	Aldabra, Thomasset
11	3.8 × 1.6 mm	2.44	2.0 mm	1.2 × 1.1 mm	6	Ile Michel
12	3.8 × 1.6 mm	2.44	2.0 mm	1.2 × 1.1 mm	6½	Aldabra, Sykes
13	3.8 × 1.6 mm	2.35	2.0 mm	1.2 × 1.1 mm	6	Ile Michel
14	3.8 × 1.7 mm	2.26	2.1 mm	1.2 × 1.2 mm	6	Aldabra (a), Sykes
15	3.9 × 1.4 mm	2.69	2.0 mm	1.2 × 1.1 mm	6½	Aldabra, Sykes
16	3.9 × 1.6 mm	2.48	1.9 mm	1.2 × 1.1 mm	6½	Anse Cedres
17	3.9 × 1.6 mm	2.48	1.9 mm	1.2 × 1.1 mm	6½	Aldabra, Thomasset
18	3.9 × 1.6 mm	2.48	2.1 mm	1.3 × 1.1 mm	6	Assumption, Sykes
19	3.9 × 1.6 mm	2.35	1.9 mm	1.4 × 1.1 mm	6¼	Platin
20	3.9 × 1.7 mm	2.30	2.1 mm	1.2 × 1.2 mm	6	Aldabra (a), Sykes
21	3.9 × 1.5 mm	2.63	1.9 mm	1.2 × 1.2 mm	6	Assumption, Sykes
22	3.9 × 1.5 mm	2.63	1.9 mm	1.2 × 1.0 mm	6¾	Anse Cedres
23	3.9 × 1.6 mm	2.52	2.1 mm	1.2 × 1.2 mm	6¼	Ile Michel
24	3.9 × 1.6 mm	2.42	2.0 mm	1.2 × 1.2 mm	6¼	Ile Michel
25	3.9 × 1.6 mm	2.42	2.1 mm	1.2 × 1.2 mm	6¼	Ile Michel
26	4.0 × 1.5 mm	2.67	1.9 mm	1.1 × 1.1 mm	6¾	Aldabra, Sykes
27	4.0 × 1.6 mm	2.56	2.0 mm	1.2 × 1.2 mm	6¾	Anse Cedres
28	4.0 × 1.6 mm	2.56	2.0 mm	1.2 × 1.2 mm	6½	Aldabra, Thomasset
29	4.0 × 1.6 mm	2.46	2.0 mm	1.4 × 1.2 mm	6	Assumption, Sykes
30	4.1 × 1.5 mm	2.70	2.1 mm	1.3 × 1.2 mm	6¼	Assumption, Sykes
31	4.1 × 1.6 mm	2.60	1.9 mm	1.3 × 1.2 mm	7	Anse Cedres
32	4.1 × 1.6 mm	2.52	2.1 mm	1.2 × 1.2 mm	6¼	Ile Michel
33	4.1 × 1.5 mm	2.75	2.1 mm	1.2 × 1.1 mm	6¾	Anse Cedres
34	4.1 × 1.5 mm	2.75	2.1 mm	1.4 × 1.1 mm	7	Anse Cedres
35	4.1 × 1.6 mm	2.64	2.0 mm	1.2 × 1.1 mm	6½	Aldabra, Thomasset
36	4.1 × 1.6 mm	2.64	2.0 mm	1.2 × 1.1 mm	6¾	Aldabra, Sykes
37	4.1 × 1.6 mm	2.54	2.0 mm	1.2 × 1.2 mm	6¼	Aldabra (a), Sykes
38	4.1 × 1.7 mm	2.44	2.2 mm	1.3 × 1.2 mm	6¼	Ile Michel
39	4.2 × 1.6 mm	2.68	2.0 mm	1.3 × 1.1 mm	6½	Aldabra, Thomasset
40	4.2 × 1.6 mm	2.62	2.0 mm	1.4 × 1.2 mm	6¾	Aldabra, Thomasset
41	4.3 × 1.6 mm	2.76	2.0 mm	1.3 × 1.1 mm	7	Anse Cedres
42	4.3 × 1.9 mm	2.23	2.3 mm	1.6 × 1.4 mm	6	Aldabra (a), Sykes
43	4.4 × 1.6 mm	2.80	2.1 mm	1.4 × 1.2 mm	6¾	Assumption, Sykes
44	4.4 × 1.6 mm	2.69	2.1 mm	1.4 × 1.2 mm	7	Aldabra, Sykes
45	4.4 × 1.6 mm	2.69	2.2 mm	1.3 × 1.2 mm	6½	Aldabra (a), Sykes
46	4.4 × 1.7 mm	2.50	2.1 mm	1.4 × 1.3 mm	6½	Aldabra (a), Sykes
47	4.4 × 1.6 mm	2.84	2.2 mm	1.4 × 1.1 mm	7	Assumption, Sykes

TABLE I (*contd*)

no.	length × maj. diam.	l/d	length	aperture	number of	locality
			last whorl	length × width	whorls	
48	4.4 × 1.6 mm	2.84	2.2 mm	1.4 × 1.2 mm	6 $\frac{3}{4}$	Assumption
49	4.6 × 1.9 mm	2.43	2.4 mm	1.6 × 1.3 mm	6 $\frac{1}{2}$	Ile Picard, Sykes
50	4.7 × 1.7 mm	2.78	2.4 mm	1.5 × 1.4 mm	6 $\frac{1}{2}$	Assumption
51	4.7 × 1.8 mm	2.59	2.2 mm	1.3 × 1.2 mm	7	Aldabra (a), Sykes
52	4.7 × 1.8 mm	2.59	2.2 mm	1.4 × 1.3 mm	6 $\frac{3}{4}$	Aldabra (a), Sykes
53	4.9 × 1.7 mm	2.82	2.2 mm	1.5 × 1.3 mm	7	Aldabra (a), Sykes
54	4.9 × 1.9 mm	2.63	2.4 mm	1.6 × 1.3 mm	7	Aldabra (a), Sykes
55	5.0 × 1.8 mm	2.76	2.4 mm	1.6 × 1.2 mm	7	Platin
56	5.1 × 1.9 mm	2.73	2.4 mm	1.5 × 1.4 mm	7	Aldabra (a), Sykes

For explanation of the localities see the text. The shells have been enumerated according to size taken from micrometer readings, which are much more accurate than their translation into mm (e.g. 62 points = 3.9 mm, but also 63 points = 3.9 mm, etc.). No. 34 is the holotype (fig. 1, BMNH); no. 49 is the 'type' of *Ennea alauda* Sykes nom. nud. Specimens nos. 5, 17, 18, and 48 show (very) faint traces of apical spiral sculpture.

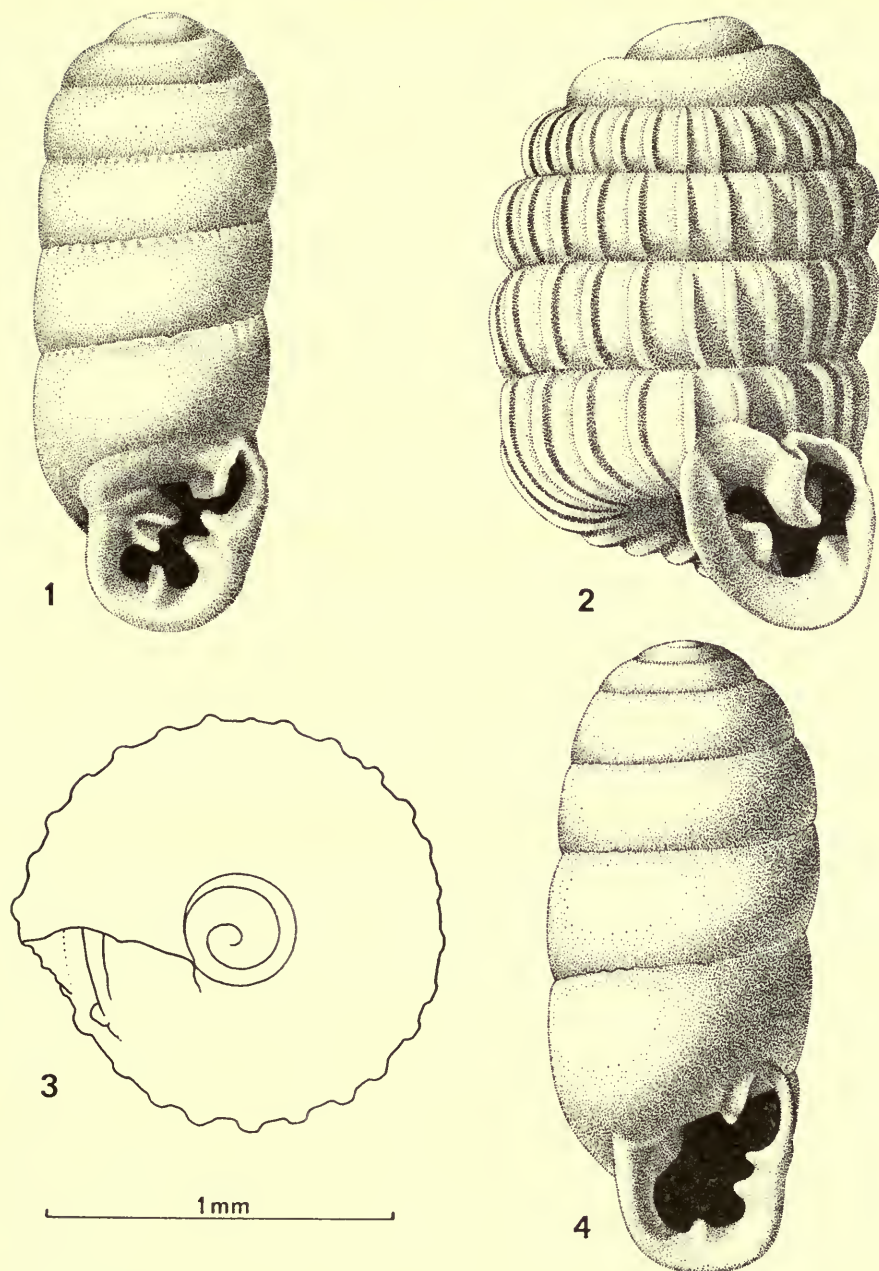
MATERIAL EXAMINED:

RECENT: Holotype, ALDABRA ISLAND: South Island (Grande Terre), Anse Cedres, c. 400 m inland (Grid ref. 359112) under stones in open grassy area amongst mature bush, 11.ix.1967, (Peake, RSE) BMNH. No. 197424. Paratypes include all material listed below, similar locality, habitat and collecting data as above, BMNH No. 197425, RMNH Nos. 54937-54939; West Island (Ile Picard), PSTE/JCFF (E. R. Sykes Colln) ['Type' of *Ennea alauda* Sykes nom. nud.], BMNH No. 197426; West Island, near village (Grid. ref. 957102), in litter around *Casuarina* trees, 7.ix.1967 (Peake, RSE), BMNH No. 197427; Ile Michel (Coconut Island, Grid ref. 325083), under stones, 14.ix.1967 (Peake, RSE) BMNH No. 197428; South Island, Platin, near pool (Grid ref. 361101), under stones, 11.ix.1967 (Peake, RSE), BMNH No. 197429; *ibid*, Platin, near runway trace (Grid ref. 363095), in litter amongst bush area, 9.ix.1967 (Peake, RSE), BMNH No. 197430.

Poorly localized material: ALDABRA, PSTE/JCFF, BMNH and RMNH, (E. R. Sykes Colln); ALDABRA, NM (vide Connolly, 1925: 265) (H. P. Thomasett, H. C. Burnup Colln); West Island and Takumaka (= Takamaka). N.B. two different localities, shown in Table 1 as 'Aldabra (a)', PSTE/JCFF, BMNH (E. R. Sykes Colln). ASSUMPTION ISLAND: PSTE/JCFF, BMNH and RMNH (E. R. Sykes Colln); Central area, 16.ix.1967 (Peake, RSE), BMNH No. 197433.

FOSSIL: ALDABRA ISLAND: Middle Island (Ile Malabar), Stn 31 (Grid ref. 301123), cavity fill deposit cut into Aldabra Limestone associated with *Tropidophora* sp., age less than 125 000 years BP and possibly 27 000 years BP (Taylor *et al*, RSE), BMNH No. 9921200; South Island, Stn 39D (Grid ref. 186024), Solution cavity fill cut into Takamaka Limestone buff 'soil' with abundant rootlets and associated fauna of *Tropidophora* and *Rachis*, age probably last glacial, that is post 125 000 years BP (Taylor *et al*, RSE), BMNH No. GG21201.

Note: Juvenile shells and fragments are expressly excluded from the type series. Material recorded, but not examined: ALDABRA ISLAND: Ile Verte (Smith, 1909: 69).



FIGS 1-4. Aldabra Island Streptaxidae. 1, *Gulella gwendolinae aldabrae* n. subsp., holotype shell, actual length 4.1 mm; 2, *G. peakei* n. sp., holotype shell, actual length 2.0 mm; 3, *G. peakei* n. sp., juvenile shell from below, to show the angular lamella in the form of a ridge extending beyond the aperture (scale applies to fig. 3 only); 4, *G. insulicola* n. sp., holotype shell, actual length 4.4 mm, broken in the process of drawing, but repaired. All figured specimens in British Museum (Natural History).

Distribution on Aldabra is shown in fig. 6.

There is little variation in the apertural dentition, except for the columellar complex, which may vary in the depth of bifurcation. There is no trace of apertural dentition in juvenile shells.

The above numerical data are for all material examined. The population on Assumption Island is presumably genetically separated from those on Aldabra Island proper. Assumption is situated roughly 30 km to the southeast of Aldabra. However, the number of shells available for Assumption amounts to only nine, so that no conclusions may be drawn. Measurements are in mm and the following data are shown from left to right: length $\times$ major diameter, l/d , length last whorl, length $\times$ width of aperture, number of specimens measured.

Aldabra: $3.6-5.1 \times 1.4-1.9$, $2.23-2.84$, $1.8-2.4$, $1.1-1.6 \times 1.0-1.4$, 47

Assumption: $3.7-4.7 \times 1.5-1.7$, $2.40-2.84$, $1.9-2.4$, $1.2-1.5 \times 1.1-1.4$, 9

Mean l/d 2.53, average l/d 2.54 (Aldabra); do., 2.62, 2.66 (Assumption). In both cases the shells have six to seven whorls. The range of measurements is on the whole smaller on Assumption, but this may reflect limitations imposed by the small sample.

The only local population on Aldabra which may enjoy a certain degree of spatial and consequently genetical isolation is that on Ile Michel or Coconut Island. Corresponding figures for this island also show a smaller range of measurements:

Ile Michel: $3.6-1.4 \times 1.6-1.7$, $2.28-2.52$, $1.9-2.2$, $1.2-1.3 \times 1.1-1.2$, 8

In this case mean and average l/d have values of 2.40 and 2.42 respectively and the shells have only $6-6\frac{1}{4}$ whorls. However, drawing of conclusions based on eight specimens again seems unwarranted. Ile Michel is only about 1 km from the nearest land, South Island (Grande Terre), so that there is really no question of effective isolation.

Smith (1909) recorded this species as '*Ennea* sp... may prove to be new'. A year later Preston (1910) described *Ennea gwendolinae* from Kenya, with which Connolly (1925) identified his Aldabra material. *Gulella gwendolinae* is known from the coastal area of Kenya (including the Shimba Hills), the Usambaras and Dar-es-Salaam in Tanzania, west of Lake Rudolf in Kenya and southeast of Lake Chad. This includes the following aberrant forms: *scissidens* Connolly, 1922 (Dar-es-Salaam); *porrecta* Pfeiffer, 1952 (Mombasa); *mkusiensis* Verdcourt, 1953 (W. Usambaras); *tsadiensis* Blume, 1959 (SE Lake Chad); var. nov. Verdcourt, 1962 (Turkana).

Notwithstanding the authority and scientific acumen of Connolly, it seems at first somewhat far-fetched to identify an Aldabra snail with a species of the African mainland. The gap between the coast of East Africa and Aldabra atoll consists of roughly 640 km of ocean, a seemingly unsurmountable barrier for a land snail. On the other hand, the character of the fauna of many islands in the western Indian Ocean is unmistakably African. The following are two quotations from Peake in Westoll & Stoddart (1971: 581-610): 'The affinities of the vertebrate fauna on all islands in the western Indian Ocean are predominantly orientated towards Africa' (p. 586); 'The fauna exhibits a wide range of affinities depending on the taxa and taxonomic levels considered; those with Africa are dominant, ...' (p. 606). Cogan,

Hutson & Shaffer in Westoll & Stoddart (1971 : 315-325) write : 'To summarize it may be said that the insect fauna of Aldabra is predominantly African in origin, . . .' (p. 324). Wright in Westoll & Stoddart (1971 : 299-313) concludes that the fresh-water snails of the genus *Bulinus* on Aldabra are also of African origin, although some may have reached the atoll via Madagascar. All this stresses African origin and derivation, but so far no non-marine molluscan species on Aldabra has actually been identified with (East) African species. This has, however, occurred in Entomostraca (McKenzie in Westoll & Stoddart, 1971), Diptera, and Lepidoptera (Cogan, Hutson & Shaffer in Westoll & Stoddart, 1971).

The Comoros are much closer to the African continent. Although no modern summary is available, it appears from a scrutiny of a series of papers by Morelet (1860-1885) and material in various collections that African species indeed do occur here.

TABLE 2

Comparison of measurements of the shells of various populations of *Gulella gwendolinae*

material	length × maj. diam.	<i>l/d</i>	aperture length × width	number of whorls	<i>n</i>
<i>aldabrae</i>	3.6-5.1 × 1.4-1.9 mm	2.23-2.84	1.1-1.6 × 1.0-1.4 mm	6-7	56
<i>gwendolinae</i>	4.8-5.4 × 1.7-1.8 mm	2.82-3.09	1.6-1.8 × 1.2-1.4 mm	7	7
<i>porrecta</i>	5.5 × 1.9 mm	2.87	1.7 × 1.4 mm	7	1
<i>tsadiensis</i>	3.6-4.6 × 1.6-1.9 mm	2.00-2.50	1.7-1.9 × 1.3-1.5 mm	5½-6	29

n = number of specimens examined. Data shown under *gwendolinae* are from the holotype in the Ter-vuren museum, four paratypes in the British Museum (Natural History), and one paratype each in the Frankfurt and Leiden museums. Data shown under *porrecta* are from the holotype in the Frankfurt museum and those for *tsadiensis* have been extracted from Blume (1959).

In Table 2 the various forms of *G. gwendolinae* are compared ; the subspecies or varieties *scissidens*, *mkusiensis* and 'var. nov.' have not been taken into account, because these are rather aberrant. The var. *porrecta* may be a synonym of the typical form (Verdcourt, 1962 : 8). A warning may be sounded as to the number of specimens considered here. This table shows that the Aldabra form is

- smaller than the typical form, but larger than *tsadiensis*, although there is a wide overlap ;
- has a smaller major diameter than both the typical form and *tsadiensis*, although there is an almost complete overlap ;
- is not as slender as the typical form, but more so than *tsadiensis*, albeit with a small overlap ;
- has a smaller aperture than both the typical form and *tsadiensis*, with small overlaps ;
- has somewhat fewer whorls than the typical form, but somewhat more than *tsadiensis*.

This shows on the whole that at least three recognizable units may be distinguished, viz. the Aldabra-Assumption populations, the typical form, and the subspecies *tsadiensis*. *Gulella gwendolinae* is a variable species with an apparently wide distribution. Verdcourt (1962 : 7, footnote) rightly advises : 'Until considerable material

is available it would be as well not to bestow more names.' However, in view of the isolated location of the Aldabra-Assumption populations, it is proposed here to separate these as the subspecies *aldabrae*. Unfortunately anatomical studies are not as yet possible because of the lack of preserved soft parts.

Gulella gwendolinae aldabrae is the only recent streptaxid on Aldabra atoll. It is reasonable to expect it to have been transported from the African mainland to the island. Aldabra has always been a remote place and in view of the noticeable differences found and fossil occurrence it is unlikely that it has arrived in the wake of Man. Also, there are no records of the species from either the Comoros or Madagascar (cf. Fischer-Piette & Bedoucha, 1964b). Dispersal by tropical storms is also unlikely because of the direction of these in the area; the animal is, however, sufficiently light to be carried by high winds. Dispersal by birds is even less likely; the snail will certainly hardly have been picked up by the birds which now populate Aldabra. Rafting may merit consideration, but there are no suitable surface currents to effect a dispersal from Africa to Aldabra. Obviously *G. gwendolinae* has good dispersal ability, a character it shares with many small terrestrial snails (cf., e.g., Carlquist, 1965: 292-293). For the time being no reasonably plausible explanation for the presence of *G. gwendolinae* on Aldabra is available.

Gulella peakei n. sp.

Figs. 2, 3, 7

DIAGNOSIS. A minute species of *Gulella* with spaced lamellae and smooth interstices on the whorls, open umbilicus, and dentition consisting of angular lamella, two labral processes and columellar lamella.

DESCRIPTION OF SHELL. Shell (fig. 2) small, cylindrical-ovoid, greatest width about the middle, with open umbilicus, costulate, creamy white. Spire produced, sides slightly to markedly convex, subparallel, apex somewhat flattened, obtusely conical. Whorls six to six-and-a-half, convex and sculptured with comparatively prominent, regular, straight and perpendicular, widely distant, costulae, interstices much wider than riblets, smooth, under high magnification very finely granulate. In front view the holotype shell shows only about eleven costulae on the part of the whorl above the aperture; the last whorl has a total of about fifteen riblets. Initial two whorls smooth, very fine granulate under high magnification; penultimate and last whorls comparatively small. Sutures shallow, simple to subcrenellate, somewhat impressed. Aperture somewhat oblique, invertedly triangular with smoothly rounded base, about as high as wide, peristome fairly thick, expanded and somewhat reflected, dentition more or less four-fold. To the right of the middle of paries a fairly large, obliquely perpendicular, angular lamella, which is nothing but a V-shaped pleat in the peristome, connected with labrum; about half-way down the labrum a superficial swelling may be interpreted as a labral process; somewhat below this, but much deeper inside the aperture, and at a slight distance from the tip of the angular lamella, a blunt inner labral process is seen, slightly above which there is a much smaller and less prominent process or mere swelling (not shown in

fig. 2 because hidden behind superficial labral swelling) ; columellar lamella large, blunt and prominent. The main inner labral process corresponds to a shallow depression on the outside of the aperture ; the columellar lamella corresponds to a shallow furrow on the left of the outside bottom of the aperture, thus adjoining the umbilicus.

TABLE 3

Measurements of shells of *Gulella peakei* n. sp.

no.	length × maj. diam.	<i>l/d</i>	length last whorl	aperture length × width	number of whorls	additional data
1	1.7 × 1.3 mm	1.30	0.8 mm	0.6 × 0.6 mm	6	—
2	1.8 × 1.3 mm	1.43	0.8 mm	0.6 × 0.6 mm	—	apex damaged
3	1.8 × 1.3 mm	1.36	0.8 mm	0.6 × 0.6 mm	6½	apex damaged
4	1.8 × 1.3 mm	1.36	0.9 mm	0.6 × 0.6 mm	6	—
5	1.8 × 1.3 mm	1.39	0.8 mm	0.7 × 0.6 mm	6	—
6	1.8 × 1.3 mm	1.35	0.8 mm	0.6 × 0.6 mm	6½	aperture rather oblique
7	1.9 × 1.3 mm	1.48	0.8 mm	0.6 × 0.7 mm	6½	—
8	1.9 × 1.3 mm	1.48	0.8 mm	0.6 × 0.7 mm	6	—
9	1.9 × 1.3 mm	1.47	0.8 mm	0.7 × 0.6 mm	6½	—
10	1.9 × 1.3 mm	1.42	0.9 mm	0.7 × 0.6 mm	6½	—
11	2.0 × 1.3 mm	1.57	0.9 mm	0.7 × 0.7 mm	6½	holotype, fig. 2
12	2.0 × 1.3 mm	1.51	0.8 mm	0.6 × 0.6 mm	6½	—
13	2.1 × 1.3 mm	1.55	0.9 mm	—	6½	aperture damaged
14	2.1 × 1.5 mm	1.45	0.8 mm	—	6½	aperture obscured by matrix matter

Nos. 1–13 are from Stn 34F, no. 14 from Stn 26F, Aldabra.

MEASUREMENTS OF SHELL: 1.7–2.1 × 1.3–1.5 mm, *l/d* 1.30–1.57 (mean 1.43, average of 14: 1.44), length last whorl 0.8–0.9 mm, aperture length × width 0.6–0.7 × 0.6–0.7 mm, 6–6½ whorls. Table 3 details the measurements of 14 adult shells ; the holotype is no. 11.

MATERIAL EXAMINED :

FOSSIL : Holotype, ALDABRA ISLAND : Middle Island (Ile Malabar), Stn 34F (Grid ref. 293109), age inferred as 27 000 BP (Taylor *et al*, RSE), BMNH No. GG21202. Paratypes, similar locality and information as above, 12 shells in good condition (2–13 of Table 3) BMNH No. GG21203 and RMNH 54940–3, 14 further paratypes in poor condition or still covered by the matrix BMNH No. GG21204, numerous juvenile shells and fragments ; South Island (Grande Terre), Stn 26F (Grid ref. 337055), age uncertain but possibly same as 34F (Taylor *et al*, RSE), BMNH No. GG21205, 1 paratype (14 of Table 3) and 3 juvenile shells.

Other material : South Island, Dune d'Messe, Stn 39A (Grid ref. 186029), age inferred as 27 000 BP (Taylor *et al*, RSE), BMNH No. GG21206, some shell fragments.

Note : Juvenile shells and fragments are expressly excluded from the type series.

Distribution (fig. 7). Quaternary of Middle Island (Ile Malabar) and South Island (Grande Terre), Aldabra Island. Dr Taylor has kindly furnished the following details on the localities where *Gulella peakei* has been obtained. Stn 26F: 'Brown cavity-fill deposit in Takamaka Limestone. Many small gastropods. Age uncertain, possibly pre-125 000 yrs.' Stn 34F: 'Cavity-fill deposit cut into the Takamaka Limestone, buff 'soil' containing abundant large ribbed *Tropidophora* (only site for this species). Abundant *Assimineae*, *Gulella* within cavities of the *Tropidophora* and in the matrix. Almost certain last glacial, post 125 000 yrs BP.' Stn 39A: 'Solution cavity-fill cut into Takamaka Limestone. Buff 'soil' with abundant rootlets and associated fauna of *Tropidophora* and *Rachis*. Age probably last glacial, post 125 000 yrs BP.'

The species has been named after Mr J. F. Peake, Deputy Keeper of Zoology and Head of the Mollusca Section of the British Museum (Natural History), as a token of friendship and admiration for his island research.

The angular lamella is present in all juvenile shells in the form of a long and conspicuous, simple, ridge, usually stretching somewhat beyond the aperture (fig. 3). Damaged shells show that this ridge is being resorbed on the one end in the course of growth while being added to at the actual aperture. No other dental processes are present in the juvenile shells. Juvenile dentition is rare among species of the genus *Gulella* and much more common among representatives of allied genera, such as *Ptychotrema* (vide, e.g., van Bruggen, 1971, fig. 2, p. 249). Among the about 125 species of *Gulella* in Southern Africa there are about three species in which this phenomenon has been described (Burnup, 1925; Connolly, 1939), although juvenile shells are as yet unknown for a number of species. At least three of the species which will be considered below when trying to assess the relationships of the new species also have juvenile shells with apertural dentition, viz. *G. jacquelineae* Adam, *G. pooensis* Ortiz de Zárate & Ortiz de Zárate and *G. spatium* (Preston) (see Adam, 1965; Ortiz de Zárate & Ortiz de Zárate, 1956; Verdcourt, 1970, the latter as interpretation of Blume, 1965).

Gulella peakei has no allies on Europa Island (so far no streptaxids have been reported from this island: Fischer-Piette & Bedoucha, 1964a; Legendre, 1966; Fischer-Piette & Vukadinović, 1971), Madagascar (Fischer-Piette & Bedoucha, 1964b), the Mascarene Islands (Germain, 1921; Connolly, 1925), the Seychelles (Sykes, 1909; Connolly, 1925; Barnacle, 1962), the Comoros (Morelet, 1860, 1877, 1879, 1881, 1882, 1883, 1885; Von Martens, 1876), or Aldabra Island (Von Martens & Wiegmann, 1898; Smith, 1909; Connolly, 1925; Barnacle, 1962). A few of the species enumerated by Morelet for the Comoros, such as *Pupa minuscula* Morelet (1877: 340, pl. 12, fig. 5), which may be a streptaxid, superficially resemble *Gulella peakei*, but never show the peculiar spaced lamellae on the whorls. As regards *Pupa minuscula* Morelet writes 'obsolete costulata', and 'Le test est orné de côtes fines, espacées sur le dernier tour'. *Gulella peakei* certainly does not have fine ribs, spaced on the body whorl, but rather shows widely spaced lamellae all over the shell except for the apex.

The new species obviously belongs to Verdcourt's 'Key 4' (Verdcourt, 1962: 8). This key features East African species with spaced lamellae on the whorls. This is

probably not a natural group, although some of the species may be allied to each other. They belong to *Costigulella* Pilsbry, 1919, *Mirigulella* Pilsbry & Cockerell, 1933, and *Aenigmigulella* Pilsbry & Cockerell, 1933; these are all considered subgenera of *Gulella* L. Pfeiffer, 1856, by Zilch in his manual (Zilch, 1959-60; see also Zilch, 1961). The subgenera *Mirigulella* (monotypic) and *Aenigmigulella* (with two species, cf. Adam, 1965: 40) are very probably products of a long and separate development; the subgenus *Costigulella* with perhaps about ten species altogether is rather an assemblage of diverse elements. A preliminary assessment of the species of *Costigulella* shows that this subgenus may consist of three groups, viz.

(a) *G. langi* Pilsbry and *G. toticostata* Pilsbry, both from the Congo (Zaire), and *G. pooensis* Ortiz de Zárate & Ortiz de Zárate from Fernando Poo, with lamellae and spiral sculpture on the whorls (*Costigulella* s.s.),

(b) the Kenya taxa *G. adjacens* (Preston), *G. spatium* (Preston), *G. p. pretiosa* (Preston) and *G. p. nyiroensis* (Preston), with costulae in between the lamellae on the whorls (see also Adam, 1965: 46, who states that all three may also have costulate early whorls), and

(c) the West African species *G. hedwigae* Degner, with smooth interstices between the lamellae on the whorls.

G. microtaenia Pilsbry & Cockerell most probably does not belong to *Costigulella* s. lat. because of the 'delicate riblets' (Pilsbry & Cockerell, 1933: 372). For the time being the present author refrains from naming the subdivisions of *Costigulella* s. lat., particularly because of the differences in dentition of the shells and the absence of anatomical data. However, zoogeographically the above three groups at first sight seem to be fairly natural: group (a) inhabits the West and Central African equatorial forest, group (b) the East African forests and group (c) the western parts of the West African equatorial forest. The subgenera *Aenigmigulella* and *Mirigulella*, both from East African forests on elevated country, may have ancestors in common with group (b). Only *Mirigulella* has a reduced dentition; the forest element is usually of a more primitive nature than species or groups outside the forest. Therefore one may be tempted to consider all above taxa (all forest dwellers in the uplands, or lower down where the forest comes down to sea level, such as on Fernando Poo) to be more primitive than *Mirigulella*.

Compared with *G. peakei* all the above species are either too large, or have a different dentition or costulation, but usually one finds a combination of all three factors. The writer has been able to study type material or other specimens of most of these species in the museums in London, Frankfurt am Main and Leiden. *G. peakei* is not to be confused with any of the species under discussion. By virtue of the absence of sculpture on the interstices between the lamellae on the whorls the new species belongs to group (c) of *Costigulella* s. lat. Zoogeographically this is a somewhat surprising conclusion, because one hardly expects a species from Liberia and one from Aldabra to have common ancestors. Of course, the minute terrestrial snails of continental Africa are still very incompletely known and *G. hedwigae* or allied species yet to be discovered may well occur further east. Apart from other considerations it seems fairly certain that the ancestor of *G. peakei* is of continental African origin. However, the possibility that a likeness to *G. hedwigae* may have been caused

by convergent evolution cannot be ruled out. Only anatomical data are likely to help solve this question; the fact that *G. peakei* is extinct will, however, frustrate such a project.

G. peakei is obviously extinct on Aldabra Island. Species resembling it are restricted to forest habitats in Africa; there is no more suitable forest habitat available on Aldabra, indeed the overall impression is that of a 'semi-arid island' (Stoddart in Westoll & Stoddart, 1971: 8). Aldabra is an elevated atoll consisting of an elevated reef situated on the summit of a mountain rising from the sea floor. There is evidence that in the past Aldabra has been much more elevated (Stoddart *et al* in Westoll & Stoddart, 1971: 31-66, and personal communication of Dr J. D. Taylor), which must have resulted in a moister climate and consequently also the presence of a type of forest suitable for species such as *G. peakei*. Some of the islands in the Western Indian Ocean still have a fair amount of forest, but so far no apparent allies of *G. peakei* have been obtained here.

Gulella insulicola n. sp.

Figs. 4, 8

DIAGNOSIS. A small species of *Gulella* with smooth whorls, open umbilicus, and dentition consisting of angular lamella, two labral processes, a basal denticle, and columellar lamella.

DESCRIPTION OF SHELL. Shell (fig. 4) small, subcylindriform, with open umbilicus, smooth, creamy white. Spire produced, sides subparallel, apex flattened, obtusely conical. Whorls six to six-and-a-half, slightly convex, almost completely smooth, only with traces of costulation or striation behind the labrum, initial whorls smooth, very finely granulate under high magnification; sutures shallow, simple, somewhat impressed, occasionally subcrenellate. Aperture subquadrate, rounded at base, peristome incrassate and reflected, white and probably glossy when fresh, with five-fold dentition: a reasonably well-developed slightly oblique angular lamella, touching or connected with the tip of the labrum; two subequal mid-labral denticles on a slightly raised common base, labral complex corresponding to very shallow external pit; a small mid-basal denticle, which usually is situated slightly to the left of the middle of the base and which may be so small as to be hardly noticeable, in which case the dentition may be interpreted as being four-fold; columellar lamella small and little prominent, blunt and fairly deep-set.

MEASUREMENTS OF SHELL: $3.9-4.4 \times 1.9-2.0$ mm, l/d 2.07-2.29 (mean 2.18, average of 4: 2.14), length last whorl 2.1-2.3 mm, aperture length $\times$ width, 1.3-1.6 $\times$ 1.2-1.3 mm, 6-6½ whorls. Table 4 details the measurements of four adult shells; the holotype is no. 4.

MATERIAL EXAMINED:

FOSSIL: Holotype, ALDABRA ISLAND: Middle Island (Ile Malabar), Stn 34F (Grid ref. 293109), age inferred as 27 000 BP (Taylor *et al*, RSE), BMNH No. 21216. Paratypes, similar locality and information as above, 4 shells (Taylor *et al*, RSE),

BMNH No. 21217. Collected together with *Gulella peakei* n. sp.; for details of locality see data under 'Distribution' for that species. All specimens are in poor condition, the shells being worn and very fragile.

Distribution (fig. 8). So far only known from the Quaternary of Ile Malabar or Middle Island.

TABLE 4

Measurements of shells of *Gulella insulicola* n. sp. from Stn 34F, Aldabra

no.	length × maj. diam.	<i>l/d</i>	length last whorl	aperture length × width	number of whorls	additional data
1	3.9 × 1.9 mm	2.07	2.1 mm	1.3 × 1.2 mm	6	—
2	4.1 × 1.9 mm	2.09	2.2 mm	1.4 × 1.3 mm	6+	apex damaged
3	4.2 × ± 2.0 mm	± 2.09	2.2 mm	1.4 × 1.3 mm	6½	body whorl damaged
4	4.4 × 1.9 mm	2.29	2.3 mm	1.6 × 1.3 mm	6½	holotype broken but repaired

The holotype shell, no. 4, was broken, but has been repaired.

The specific name *insulicola* is a noun derived from *insula* (Lat.: island) and *icola* (Lat.: inhabitant).

The new species represents a common pattern in the genus *Gulella*. Taxa with a smooth shell and a five-fold dentition have been brought together for Southern Africa by Connolly (1939: 20) as group 4 (ii) (10 species) and the East African ones are treated by Verdcourt (1962: 20) in part of Key 4 (9 species). Many of these species show a dental pattern similar to that of *G. insulicola*. Among the island dwellers *G. poutrini* (Germain, 1918), which is common on Mauritius, and *G. comorensis* (von Martens, 1876) of the Comoros exhibit the same pattern. Comparison with species with the combination of characters as described above has failed to provide satisfactory identification, so that we may conclude that *G. insulicola* represents indeed a hitherto undescribed species. Its closest allies are perhaps the above species from Mauritius and the Comoros; these differ from the new species in being much larger (sometimes twice as large), having more whorls and being less slender than *G. insulicola*. Perhaps the group with a smooth shell and a dental pattern consisting of angular lamella, two labral processes, a basal denticle, and a columellar lamella, is a natural one distributed over much of West, Central, East and Southern Africa, and on the islands in the Western Indian Ocean as well. The possibility that *G. poutrini* and *G. comorensis* may be the components of a superspecies or represent the subspecies of a widely-dispersed species may be merely food for thought in this respect. On the other hand, a shell type such as has been discussed here occurs throughout the genus *Gulella* and may well be the result of convergent evolution.

G. insulicola is obviously extinct on Aldabra, which may also be due to the fact that suitable habitat has disappeared in the course of the process of the island becoming progressively drier.

Gulella spec.

There are two specimens (BMNH) which represent a fourth species of the genus *Gulella*. Both are clearly fossils. The one, from 'Stn 34F' (see sub *G. peakei* sp. n.), is a juvenile shell of 3.2×2.0 mm with five whorls, of which the initial ones are smooth and the others sculptured with somewhat undulating costulae. The other

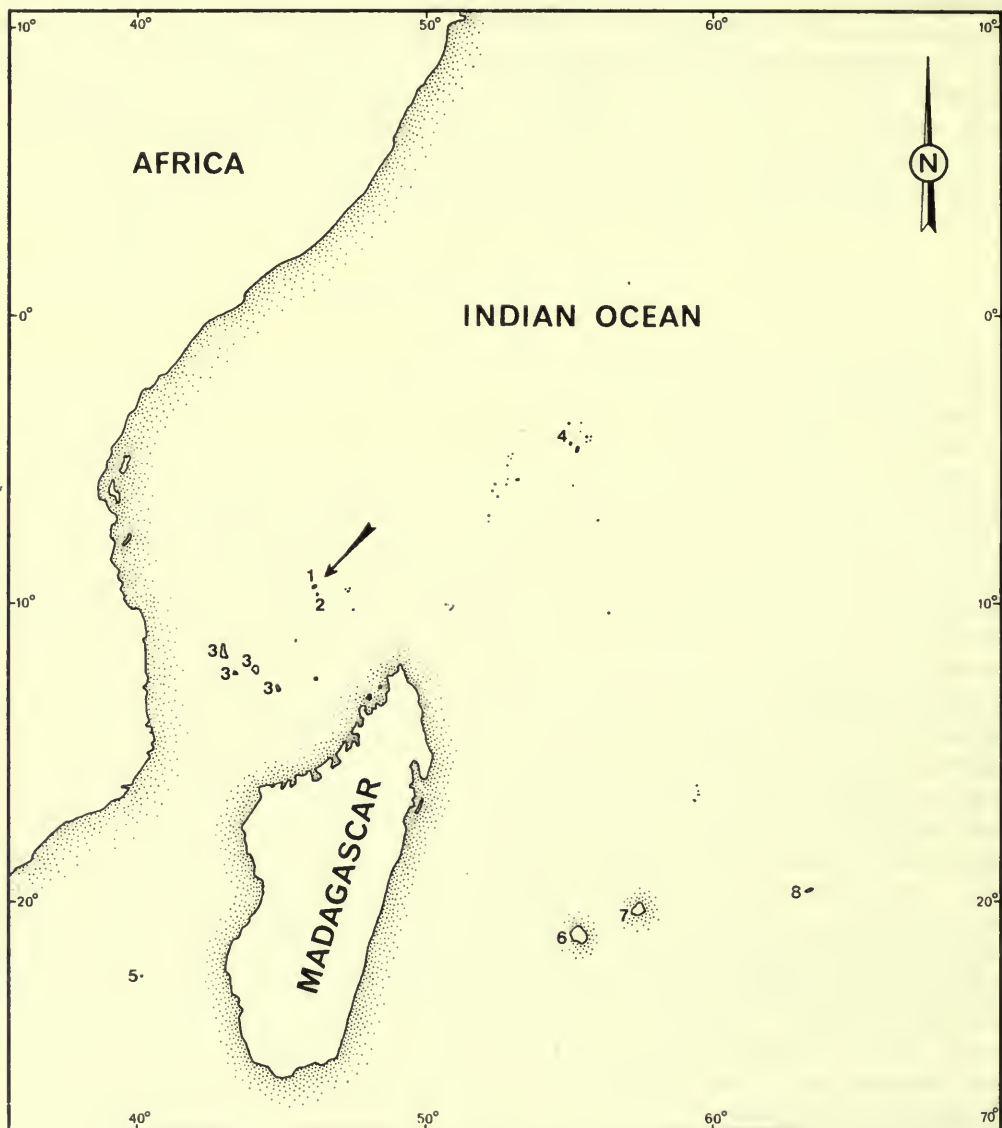


FIG. 5. Map showing position of Aldabra Island. 1, Aldabra; 2, Assumption; 3, Comoros; 4, Seychelles; 5, Europa; 6, Reunion; 7, Mauritius; 8, Rodriguez (6-8 Mascarenes).

specimen is a much younger juvenile shell of probably the same species ; it measures only 2.3 mm and the aperture is filled with matrix matter. This shell was obtained not far from the settlement on West Island (Ile Picard), grid ref. 063 E-098 N (fig. 8), 'cavity-fill cut into Basin Cabris calcarenites and Takamaka limestone, 'white soil' also containing *Rachis* and *Tropidophora*. Age uncertain ; could be the same as 39A and D'. (Notes supplied by Peake and Taylor ; Stns 39A and 39D have been described above under the other species.) No opinion as regards identity of the present species is ventured here : it is most likely that this is also an extinct species.

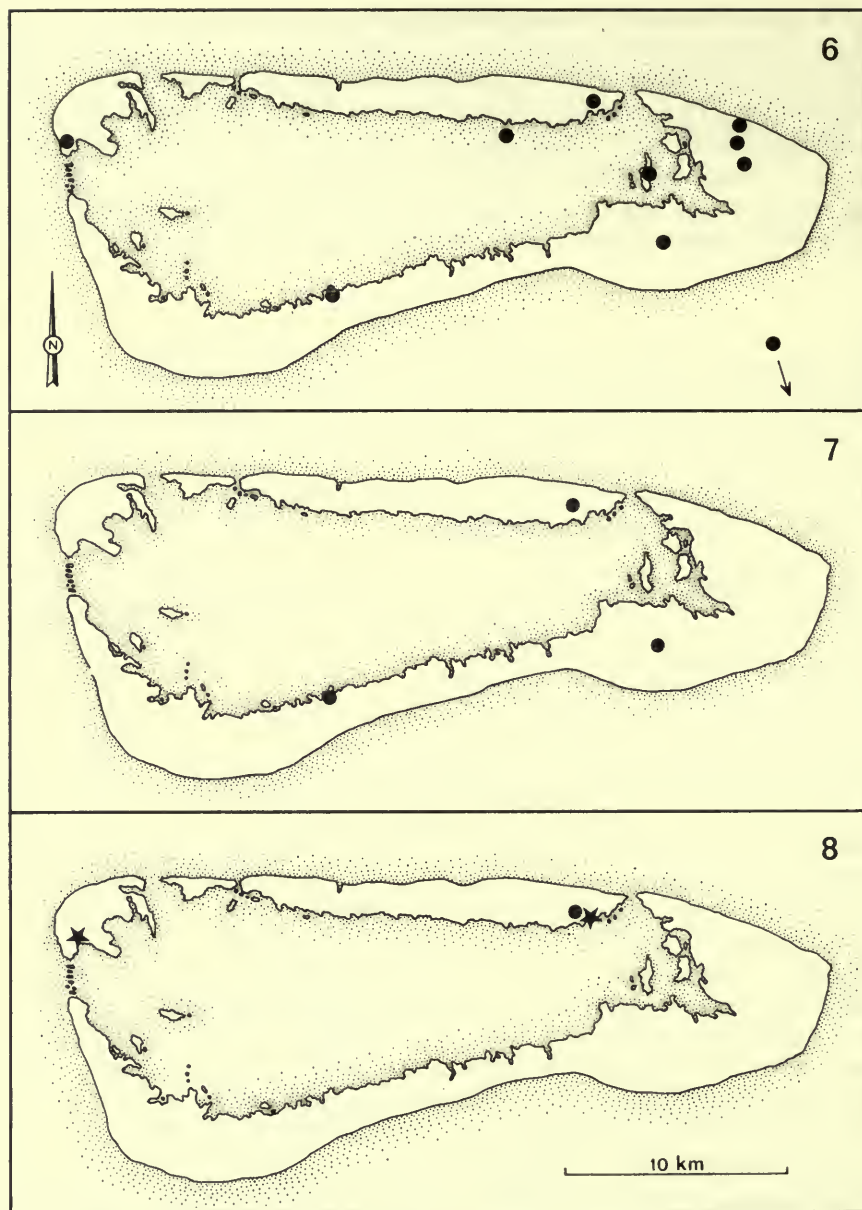
DISCUSSION

A thorough survey of the terrestrial molluscs of Aldabra has revealed the presence of four species of Streptaxidae, viz. *Gulella gwendolinae aldabrae* n. subsp., the only Recent representative of the family on the island, and three extinct taxa, *G. peakei* n. sp., *G. insulicola* n. sp. and an incompletely known species, *G. spec.*

The family Streptaxidae has excellent dispersal abilities, at least in the Western Indian Ocean. Streptaxids have reached both the Seychelles and the Mascarene Islands at distances of 1400 and 2500 km from the African mainland respectively. The Mascarene Islands are also situated between 700 and 1300 km from Madagascar from whence some streptaxid ancestors may have been derived (fig. 5). Asia (India) is more than 2500 km from the Seychelles and there are few direct relationships (if any) with the streptaxids of that continent.

G. gwendolinae is a very widely dispersed African species with a tendency to become locally separated into reasonably recognizable subspecies. Its dispersal abilities are sufficiently illustrated by its wide distribution on Aldabra and Assumption (fig. 6) ; moreover, it is also locally abundant – sufficient reason to consider it a successful species in an evolutionary sense. Perhaps the adaptability to widely divergent climatic conditions and types of vegetation has been the key to its success in Africa, which at the same time has accounted for its continued survival on Aldabra. Fossil occurrence shows that it has been on the atoll for a long time, very probably having been already a contemporary of the extinct *G. peakei*, *G. insulicola* and *G. spec.* Streptaxids are carnivores known to feed on soft invertebrates, mainly other terrestrial molluscs, and particularly snails of the pulmonate family Subulinidae (van Bruggen, 1967 : 186), which family is not (yet?) known to occur on Aldabra. However, there are Subulinidae on the high islands of the Western Indian Ocean. There are a few other land snails on the atoll, of which the enid *Buliminus* (*Rhachis*) *aldabrae* von Martens, 1898, is 'The most common of all the species from Aldabra.' (Smith, 1909 : 70 ; see also Connolly, 1925 : 264–266). Fossil evidence indicates that many terrestrial snails were contemporaries of *G. peakei*, *G. insulicola* and *G. spec.*

G. peakei, *G. insulicola*, and *G. spec.* are extinct and may well have been inhabitants of types of vegetation which have disappeared on Aldabra. The relatives of at least *G. peakei* are restricted to forest habitats such as are no longer available on Aldabra. There are still remnants of forest on high islands, e.g. the Comoros, Seychelles and Mascarene Islands, of which the latter two have species of *Gulella*



FIGS 6-8. Maps showing the distribution on Aldabra Island of 6, *Gulella gwendolinae aldabrae* n. subsp. (the arrow points to Assumption) ; 7, *G. peakei* n. sp. ; 8, *G. insulicola* n. sp. (dot) and *G. spec.* (asterisks).

which may be the nearest allies of *G. insulicola*. This species or its ancestors may therefore have arrived secondarily from these islands, although Aldabra is closer to the African continent than both the Seychelles or the Mascarene Islands. There is

also other evidence that Aldabra once harboured a much more varied flora with forest components and that a progressive drying out of conditions has caused these to disappear together with the forest dwellers among the animals that led a sheltered life in the then available leaf mould. This has caused some of the predators, the three *Gulella* species, and perhaps also their prey, species of the family Subulinidae, to disappear for ever.

Finally one has to consider how the streptaxids have reached remote Aldabra. The island has never been connected with the African continent, but Aldabra streptaxids have strong links with those from that continent. Dispersal through human agency, by tropical storms, by birds, and by rafting have all been ruled out when *G. gwendolinae aldabrae* was discussed above. The same applies, *mutatis mutandis*, for the extinct species. Yet, much of the present flora and fauna of Aldabra atoll or their ancestors have obviously come from Africa. Perhaps dispersal along the usual paths has taken place in the past when the direction of wind and surface currents was more favourable to such a process than today.

The present article was finalized early in 1973. Therefore the following comprehensive paper on the land molluscs of the Comoros has not been taken into account: Fischer-Piette, E. & Vukadinovic, D. 1974. Les mollusques terrestres des Iles Comores. *Mem. Mus. natn. Hist. nat. Paris* (N.S.) (A) **84**: 1-76. The checklist includes various African species. The family Streptaxidae appears to occupy a dominant position with 46 species. *Gulella gwendolinae aldabrae* n. subsp. should be compared to *G. dentiens* (Morelet, 1883) as figured by Fischer-Piette & Vukadinovic (fig. 18 on p. 59).

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RAAMSTEEG 2

LEIDEN

HOLLAND

QUICKIA ALDABRAENSIS (MOLLUSCA, GASTROPODA: PULMONATA, SUCCINEIDAE), A NEW SPECIES OF LAND SNAIL FROM ALDABRA ATOLL, WESTERN INDIAN OCEAN

By C. M. PATTERSON

INTRODUCTION

THE Succineidae, a rather diverse land snail family, currently includes 12 recent genera (Patterson, 1971, 1973a). *Succinea*, *Oxyloma* and *Catinella* have received the most attention by researchers, while representatives of the remaining genera have scarcely been studied. *Quickia* is distinguished from other succineids by the position of the right tentacular assembly (situated entirely to the inside of the terminal genitalia) combined with the lack of a penial sheath and penial appendix. Some unique features of *Quickia* were first reported by H. E. Quick (1936), but the genus was not named formally until 14 years later by Odhner (1950). The distribution of *Quickia* given by Odhner was '... from Liberia to the Cameroons and Gabon, on Prince Island and San Thome to East Africa (Zanzibar and Mauritius, as well as, according to Madge, 1938, Rodriguez, Reunion and the Seychelles).' Subsequently, *Quickia* received no further attention until the reproductive anatomy and chromosome number of *Q. spurca* (Gould) was described (Patterson, 1968). Following that, the existence of *Quickia* in India was reported in a morphological and cytological study of two Indian species (Patterson, 1970). In addition to its unique genital morphology, *Quickia* is of cytological interest because all five species studied have 25 pairs of chromosomes, the highest number known in the Succineidae.

The objectives of this report are (1) to describe a new species of *Quickia* from the Indian Ocean island (atoll) of Aldabra and to record its chromosome number; (2) to briefly review the distribution of *Quickia* and (3) to discuss some aspects of the biology and systematics of the genus.

MATERIALS AND METHODS

Several living specimens of *Quickia aldabraensis* were forwarded to me by C. A. Wright of the British Museum (Natural History) in January 1968. Eleven successive generations were produced during the following two years. Methods of laboratory culture are described in Patterson (1971, 1972). The following locality data and habitat description were provided by J. F. Peake (personal communication) also of the British Museum (Natural History). The specimens were collected by J. D. Taylor while participating in the Royal Society Expedition (1967-68) to Aldabra Atoll. The snails were found on the plain area at the eastern end of South Island (Fig. 1) where the surface limestone is impervious to rain water. They were observed

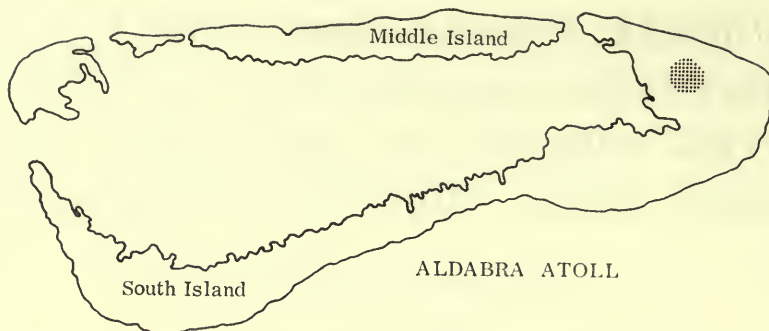


FIG. 1. Collecting site for *Quickia aldabraensis*.

variously in areas of short grass, bare rock or close to pools of fresh or somewhat brackish water. They were also found hidden under rock slabs, in cracks or other places of probable protection from desiccation. The climate of Aldabra Atoll is dry for most of the year with a short wet period which does not necessarily occur regularly.

Dissections of relaxed, alcohol-preserved specimens were made under $120\times$ or $250\times$ magnification using a Wild M5 stereoscopic microscope. All drawings were prepared with the aid of a camera lucida attachment. For details of specimen preparation and dissection see Patterson (1971).

SPECIES DESCRIPTION AND OBSERVATIONS

Quickia aldabraensis, sp. n.

Shell

Shells from both field-collected and laboratory-reared *Quickia aldabraensis* vary from attenuate to somewhat more ovate (Plate 1 and Figs. 3, 4). The same kind of variation was noted among *Q. spurca* shells (Patterson, 1968). The attenuate form of adult laboratory-reared *Q. aldabraensis* has three whorls and measures 8.5–9 mm in height and 4.5–5 mm in width. The teardrop-shaped aperture is 5.75–6 mm high and 4 mm wide. More ovate shells measure 8.5–9 mm in height, 5.5–6 mm in width and have an aperture 6 mm high and 4 mm wide. The largest shells may reach a height of 10 mm. Large adult shells collected from the field (Fig. 3) were comparable in size to those reared in the laboratory. Shells cleansed with sodium hypochlorite have a translucent light amber colour. Mud was adherent to most shells obtained from the field and appeared to be arranged in three spiral ridges on some specimens while no definite arrangement was discernible on others. Mud ridges were not present on shells of laboratory reared snails. Fine growth lines provide a minimal amount of shell sculpture. The outer shell surface is dull but the inside is very glossy. There is a well-defined columellar plait and a weakly developed, untwisted columellar fold. The peripheral margin of the shells is rounded with moderately impressed sutures. The holotype (Plate 1) is deposited in the mollusc collection of the British Museum (Natural History) (BMNH No. 1973103). Paratypes (both field collected and laboratory reared) are deposited in the mollusc

collections of both the British Museum (Natural History) (BMNH No. 1973104) and the University of Michigan, Museum of Zoology.

Jaw

The jaw is small but relatively strong. Jaw colour varies from a medium brown to a translucent amber, with darker brown markings on the cutting piece and basal accessory plate (Fig. 5). It is higher than wide when measured at its greatest dimensions. The arms of the cutting piece are rounded with tapering anterior extremities which bend toward the central longitudinal body axis. The anterior margin of the cutting piece is deeply convex with a median prominence varying from scarcely noticeable to conspicuous. The sides of the accessory plate slant slightly inward and the posterior margin is nearly straight with rounded corners.

Radula

The radula formula for *Quickia aldabraensis* is 14-15:8-9:1:8-9:14-15. There are usually 8 lateral and 14 marginal teeth. The radula has typical succineid-like features (see Patterson, 1971) and possesses no especially distinctive characters.

External body morphology

The body of living *Quickia aldabraensis*, especially the head-foot region, has a strikingly red coloration. However, all the red colour is lost in alcohol preservation. In both living and preserved snails, the internal organs positioned within the head-foot are visible through the body wall. Black pigmentation on the head-foot and anterior mantle border varies from almost none to a maximum amount shown in Fig. 6. The kidney, visible through both the body wall and shell, is yellow in colour, bi-lobed on the animal's left side and has the shape shown in outline on Fig. 6. The foot of adult, relaxed and preserved specimens is 10-11 mm in length and 4.5-5 mm in width.

Reproductive anatomy

A ventral view of the preserved reproductive system of *Quickia aldabraensis* is shown in Fig. 7. The ovotestis is of moderate size and consists of 70-80 acini. It has a dull, light beige coloration. The ovotestis duct is very narrow as it departs from the ovotestis and has a white colour. It soon becomes distended to serve as the seminal vesicle along most of its length. The seminal vesicle portion is usually coiled once and folded three times along its length. The duct again becomes a narrow channel as it opens into the upper portion of the sperмовидuct. There are two subequal, narrow receptacula seminis and a well-developed fecundation pouch (Fig. 8). Both have a translucent white colour. The cream-coloured albumen gland is of moderate size, has a linguiform shape and follicular appearance. The tubules of the albumen gland are approximately one-half the size of ovotestis acini. The sperмовидuct and oviduct have a creamy colour and are compactly folded along their length. The inner folds of tissue along the uteral portion of the oviduct are visible through the duct wall. The spermatheca is nearly spherical, of moderate size and cream coloured. Its duct passes along the proximal ventral wall of the uteral portion of the oviduct, courses anteriorly and joins dorsally with the oviduct

at a level slightly posterior to the end of the penis (Fig. 9). Thus, the vagina is quite short in this species. The walls of the anterior portion of the oviduct and vagina become thicker and somewhat muscular in appearance. The prostate gland is of moderate size and white in colour. It is composed of a rather loose collection of tubules (Fig. 10) which were not separable into distinct bunches as in *Q. spurca*. There are many channels opening from the prostate gland into the vas deferens (Fig. 10). The vas deferens passes ventrally and anteriorly from the end of the prostate gland. It then passes dorsally over the oviduct and inserts at the apex of the penis. The penis is a simple sheathless tube approximately 1 mm in length (Fig. 9). It is situated on the right of the vagina in ventral view (Fig. 7). A cross-section shows the inner folds and the lumen of the penis (Fig. 11). The long, thin penial retractor muscle originates adjacent to the vas deferens, passes under the right tentacle assembly and courses posteriorly to its insertion in the tissue covering the anterior portion of the digestive gland. The common reproductive channel (Fig. 7) is usually equal to, or occasionally shorter than, the length of the penis. It has a muscular appearance and opens to the exterior via the oval-shaped genital aperture (Fig. 9).

Chromosome number

The haploid chromosome number of *Quickia aldabraensis* is $n = 25$, the same number observed in *Q. spurca*, *Q. bensoni* and *Q. calcuttensis*, as well as in members of two other unidentified *Quickia* from Tamilnadu, India. Fig. 2 shows a camera lucida drawing of a cell in late meiotic diakinesis. There were no chromosomal anomalies observed in any cells and chromosome pairing appeared to be completely normal.

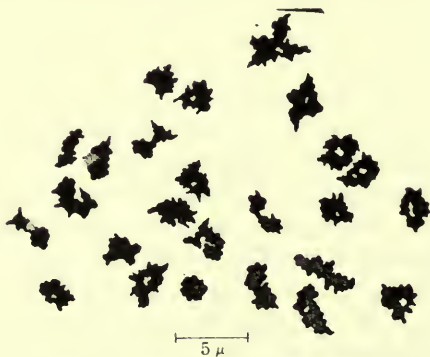
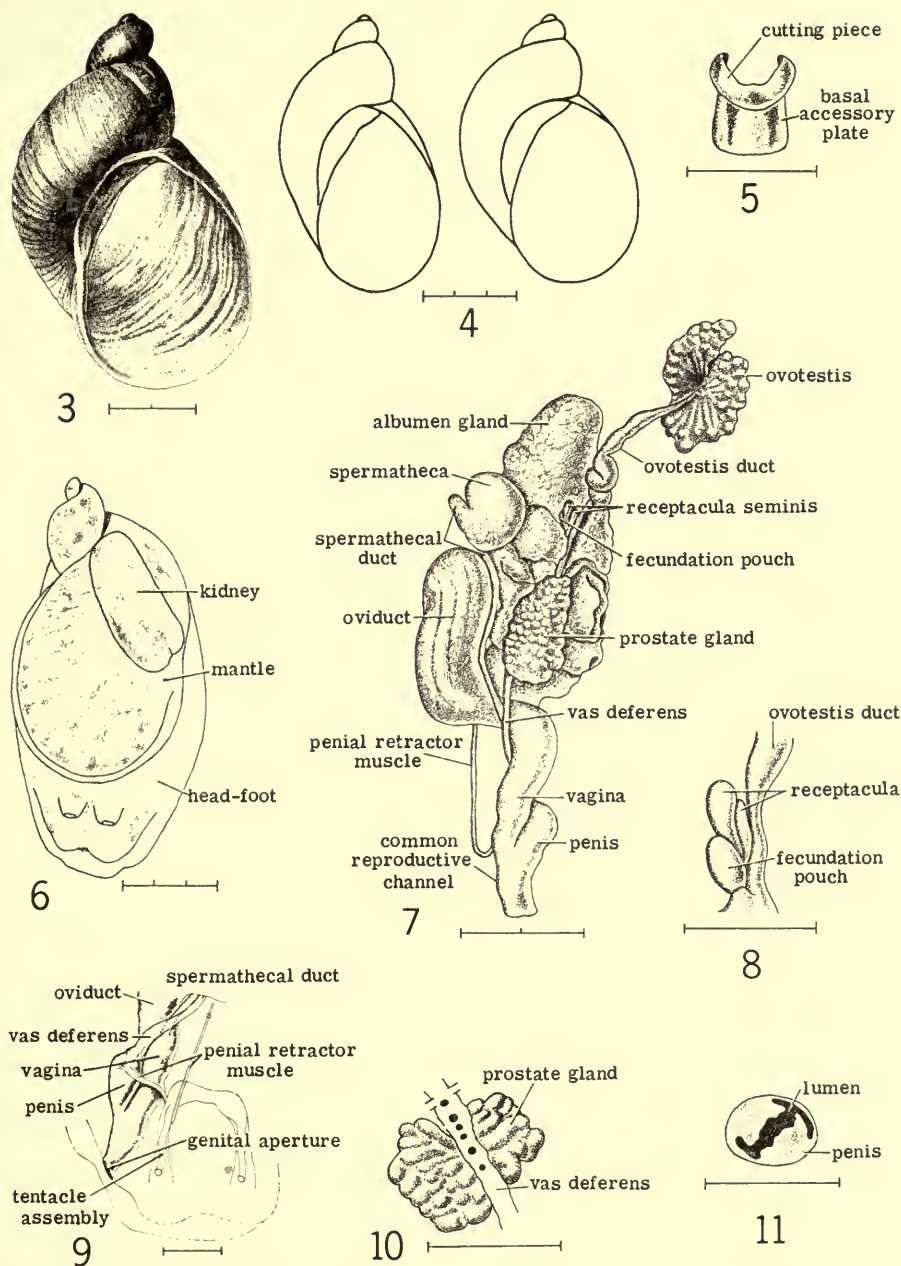


FIG. 2. Meiotic chromosomes of *Quickia aldabraensis*.

DISCUSSION AND TAXONOMY

Prior to 1968, the genus was considered to be monotypic, containing only the type species, *Quickia concisa* (Morelet). Subsequently, '*Succinea*' *spurca* Gould, '*Succinea*' *bensoni* Pfeiffer and a recently discovered Indian species (*Q. calcuttensis* Patterson) have also been found to belong to the genus *Quickia*. *Q. aldabraensis* is now the fifth species included in the genus. The Liberian *Q. spurca* differs in several respects



FIGS 3-11. 3, Shell drawing; 4, Shell shape variability; 5, Jaw; 6, Body pigmentation; 7, Ventral view of the reproductive tract; 8, Receptacula complex; 9, Terminal genitalia; 10, Prostate gland; 11, Cross section of the penis.

from *Q. concisa* (Morelet) (Patterson, 1968, 1971). However, *Q. spurca* and *Q. concisa* appear to be more closely related to each other than *Q. aldabraensis* is to either. For comparative purposes, Table 1 gives a short summary description of various distinct morphological and anatomical characters of these three species.¹

TABLE 1
Morphological characters of *Quickia*

character	<i>Q. aldabraensis</i>	<i>Q. spurca</i>	<i>Q. concisa</i>
shell sculpture	non-granulate	granulate	granulate
shell colour	amber to reddish amber	white	white
radula formula	14-15:8-9:1:8-9: 14-15	12-14:9-10:1:9-10: 12-14	11:10:1:10:1
head-foot colour	reddish	translucent white	translucent white
prostate gland	white; branching tubules; relatively large	white; loosely branching tubules; small	yellow; small
receptacula seminis	highly subequal	slight subequal to equal	slightly subequal to equal
penis position (ventral view)	right of vagina	usually left of vagina	left of vagina
penial retractor muscle insertion	posteriorly	posteriorly	anteriorly

Connolly (1925) mentioned the collection of *Succinea mascarenensis* Nevill (Morelet) Nevill from Grand Terre, Aldabra Island. Apparently this is the only occasion of assigning a name to the Aldabran succineid. Madge (1938) correctly established that '*S. nevellei* Crosse' and '*S. mascarensis* Nevill' are synonyms of '*S. concisa*'. He further stated that '*S. mascarenensis* Nevill (Morelet)' is probably also a synonym of '*S. concisa*'. However, the name *mascarenensis* used by Morelet (1882) does not have validity since his name was an alteration of Nevill's name *mascarensis* and, according to Madge (1938), was based on a mis-identification because the specimens were not comparable to those of Nevill. *Quickia aldabraensis* is thus the second valid species of the genus known to inhabit Indian Ocean islands.

The presence of mud ridges on shells of *Quickia concisa* has, in the past, been a key character used in its identification. However, the presence of mud ridges on shells of live field-collected *Q. aldabraensis* indicates they cannot be used as a valid species

¹ Descriptions of *Q. concisa* are taken from Quick (1936) and Odhner (1950). I have verified the anterior insertion of the penial retractor muscle in *Q. concisa*, but the specimens were otherwise unsuitable for a more complete anatomical study.

specific character of *Q. concisa*. From my examination of a specimen of *Q. concisa* from Rodriguez and published results of Quick's (1936) observations of *Q. concisa* from various localities, the most reliable species specific character for *Q. concisa* is the anterior insertion of a short penial retractor muscle. *Q. concisa* appears to be the only succineid species, studied to date, with such a condition. Based on present information, the accompanying key indicates the most reliable characters for identification of currently recognized *Quickia* species.

All species of *Quickia* are distinct, although *Q. bensoni* from India and *Q. spurca* from Liberia, while being the most widely separated geographically, appear to be the most closely related (morphologically) of the species. There is an indication that *Q. concisa* is rather distantly related to *Q. spurca* and *Q. bensoni*. *Q. calcuttensis* and *Q. aldabraensis* have evolved to be most different from the other species. It is difficult at this time to ascertain the relationship between the latter two species.

Quickia has the highest chromosome number known in the family Succineidae. Data for the Subclass Euthyneura indicate that generally higher chromosome numbers are associated with snail taxa which are considered morphologically more advanced by systematists (see Burch, 1965; Patterson, 1969). Odhner (1950) stated that '*Quickia* and *Indosuccinea* evidently both represent a more primitive stage of the male genital development than exists in the other species of the Catinellinae and indeed the most archaic type of male organ in any of the Succineidae hitherto examined'. One is now forced to consider whether simplification of the terminal reproductive system is instead a morphologically more advanced stage of evolutionary development which was accompanied by an increase in chromosome number derived through aneuploidy over a long period of time. *Indosuccinea* has a more simplified terminal male genital development but a lower chromosome number ($n = 24$) than *Quickia*. *Indosuccinea* could have experienced an aneuploid reduction of one (or more) bivalent(s) from a higher chromosome number or evolved in its own direction from a predecessor with a lower chromosome number. The question of the evolutionary relationship of the various succineid genera is unsettled, especially in the Catinellinae (see Patterson, 1972).

KEY TO QUICKIA SPECIES

1a	Penial apron present.	.	.	.	.	.	.	.	Subgenus <i>Burchella</i>
									<i>Quickia calcuttensis</i> Patterson
1b	Penial apron absent.	.	.	.	.	.	.	.	Subgenus <i>Quickia</i> s. s.
2a	Shell amber and without granulations.	.	.	.	.	.	.	.	2
2b	Shell white and granulate.	.	.	.	.	.	.	.	<i>Q. aldabraensis</i> sp. n.
3a	Penial retractor muscle inserts anteriorly.	.	.	.	.	.	.	.	3
3b	Penial retractor muscle inserts posteriorly.	.	.	.	.	.	.	.	<i>Q. concisa</i> (Morelet)
4a	Tubules of prostrate gland very loosely organized.	.	.	.	.	.	.	.	4
4b	Tubules of prostrate gland more compactly organized.	.	.	.	.	.	.	.	<i>Q. spurca</i> (Gould)
									<i>Q. bensoni</i> (Pfeiffer)

DISTRIBUTION AND BIOLOGY

Fig. 12 shows the known distribution of *Quickia*. *Q. concisa* appears to have the broadest distribution. However, anatomical validation of the species from many areas is necessary to substantiate such a vast distribution determined largely from

identifications often based only on shell characters. There are no records of the occurrence of *Q. aldabraensis* on any island in the Indian Ocean other than Aldabra Atoll. It would be interesting to know if additional *Quickia* species have evolved in other island groups.

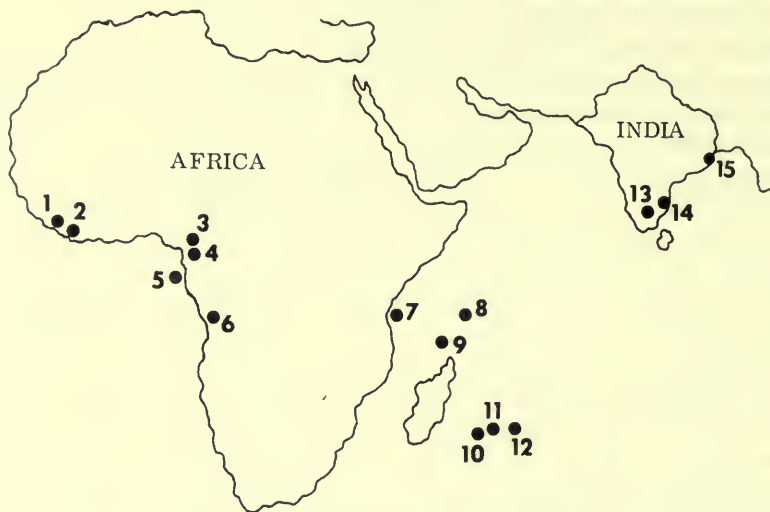


FIG. 12. Distribution map of *Quickia*.

- *1, Sierra Leone
- 2, Liberia
- *3, Cameroon
- *4, Gabon
- *5, San Thome

- *6, Angola
- *7, Zanzibar
- *8, Seychelles
- 9, Aldabra
- *10, La Réunion

- *11, Mauritius
- *12, Rodriguez
- 13, Tamilnadu State
- 14, Tamilnadu State
- 15, Calcutta

* Denotes localities for *Quickia concisa*.

Most succineids occupy relatively damp or humid habitats, some near sources of permanent fresh water. Two species (*Lithotis rupicola* Blandford and *Succinea bernardii* Récluz) are actually found in running water of falls (Patterson, 1973b). Some tropical succineids are arboreal. *Quickia* is interesting because some of its species are adapted to areas devoid of permanent standing or running water. These species depend only on seasonal rains for moisture. Usually the snails are found on rocks or rock walls or in crevices where they seek shelter in hot, dry weather. Apparently they are able to aestivate for long periods of time (one year or more) in the absence of monsoon rains. *Q. calcuttensis* from Calcutta and two other populations of *Quickia* located in Tamilnadu (Madras), India do inhabit moist areas adjacent to sources of permanent fresh water. Because of its adaptability, *Quickia* has been able to colonize areas which would seem to be unsuitable habitats for succineids. Further zoogeographical studies may reveal a much wider distribution of *Quickia*. It would be particularly interesting to know if *Quickia* occurs in Australia or if the Australian succineids living in dry habitats (i.e. *Arborcinia*) are related to *Quickia*.

ACKNOWLEDGEMENTS

I am indebted to The Royal Society for assistance and cooperation. Thanks are due to John Taylor and C. A. Wright of the British Museum (Natural History) for collecting and sending the specimens of *Q. aldabraensis* to me. I would also like to express my appreciation to John Peake also of the British Museum (Natural History) and J. B. Burch of the Museum of Zoology, University of Michigan for critically reading the manuscript and for their many kindnesses during the study.

SUMMARY

- (1) A morphological-anatomical description of *Quickia aldabraensis*, a new species from Aldabra Atoll, is presented.
- (2) The chromosome number of *Q. aldabraensis* is $n = 25$, the same number characteristic of other *Quickia* species.
- (3) *Quickia* occurs in Africa, on some Indian Ocean islands and in India.
- (4) Based on morphological studies, *Quickia* species do not seem to be particularly closely related to each other.
- (5) Members of the genus *Quickia* occupy a variety of habitats including those which are extremely dry while other species are found near areas of permanent fresh water.

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PLATE 1

Holotype of *Quickia aldabraensis*

a, Holotype (BMNH No. 1973103) collected from the type locality (1968).

b, Paratype (BMNH No. 1973104) laboratory reared. Measurement line in mm.



NOTES ON SOME ECHINODERMS FROM MARION ISLAND

By F. W. E. ROWE & A. M. CLARK

THE specimens which form the basis of the present report were collected at Marion Island in the Southern Ocean (approx. 47° S, 37° E) by Mr A. F. de Villiers during the 1972/73 South African Expedition sponsored by the Department of Transport at Pretoria and sent to the British Museum for identification.

Marion and the adjacent Prince Edward Islands were the subject of another South African expedition in 1965/66, the holothurians from which were reported on by Pawson and the other echinoderms by Bernasconi in 1971. Both these authors remark on the zoogeographical affinities of the fauna with that of Kerguelen to the east and the sub-Antarctic Falkland–Magellan area further away to the west.

The single species of holothurian taken is discussed here by F. W. E. Rowe and the remaining echinoderms by A. M. Clark.

HOLOTHURIOIDEA

Pseudocnus laevigatus (Verrill)

Pentactella laevigata Verrill, 1876 : 68.

Cucumaria serrata var. *marionensis* Théel, 1886 : 74–75, pl. 4, fig. 3.

Cucumaria laevigata : Ekman, 1927 : 396–403, fig. 15.

Pseudocnus laevigatus : Pawson, 1968 : 145, figs 2–11 ; 1971 : 288–289.

MATERIAL TVLT 7 and 28, under boulders at the sub-littoral fringe and at 4 m ; 4 specimens.

LD 11, undersides of stones at LWS ; 7 specimens.

Z 9, undersides of holdfasts of the bull kelp *Durvillea antarctica* at LWN ; 2 specimens.

Z 32, in a 'lithothamnion'-filled depression at LWS ; 6 specimens.

The size of the specimens ranges from length : breadth 8 : 3 mm to 60 : 5 mm. The majority are strongly contracted. Their colour varies from white to light pink. The ten tentacles are more or less equal. The density of the spicules of the body wall increases posteriorly. The spicules are more or less cone-shaped, ranging generally from 90 to 120 μm $\times$ 50 to 70 μm , though in one specimen (length : breadth 18 : 3 mm) the largest spicules measure 150 μm $\times$ 90 μm . The average size is 110 μm $\times$ 50 μm . Unfortunately in many cases the spicules have been eroded by initial storage in formalin. However, the complete spicules compare closely with those figured by Pawson (1968) from what he considers to be the type specimen of *Pentactella laevigata* Verrill from Kerguelen, though the present specimens are all much smaller. Similarly, direct comparison of the spicules of these Marion Island specimens with those from syntypes of *Cucumaria serrata* var. *marionensis* Théel in

the British Museum collections confirms that Ekman (1927) was correct to treat Théel's *C. serrata* with its varieties as conspecific with *P. laevigata* Verrill.

Dissection of several specimens shows that hermaphrodite gonads are present in specimens over 15 mm length (partly contracted), though the egg follicles are empty in the smaller individuals and I doubt whether even the larger specimens are fully mature. No brood pouches are present and only in the largest syntype of *C. serrata* var. *marionensis*, at c. 40 × 9 mm contracted, could I find one.

There are four polian vesicles in these specimens. Verrill (1876) noted three in his specimen and Pawson (1968) found two in specimens from Macquarie Island. I have found two to four in the syntypes of *C. serrata* var. *marionensis*.

OPHIUROIDEA

Amphiura tomentosa Lyman

Amphiura tomentosa Lyman, 1879: 23, pl. 11, figs 299–301; 1882: 132–133, pl. 29, figs 10–12. *Nullamphiura marionis* Bernasconi, 1968: 56–58, 2 figs; 1971: 286, pl. 85, fig. 4, pl. 86, fig. 2.

MATERIAL Z 25, underside of a stone in a pool connected to the sea by a tunnel; 1 very small specimen.

Z 39, in detritus under boulders at LWS; 2 specimens.

Z 55 (pt), in holdfasts of the giant kelp *Macrocystis pyrifera*; 3 specimens.

Comparison of this material with the holotype of *Amphiura tomentosa* Lyman, collected at Kerguelen by the 'Challenger', shows no significant difference that cannot be attributed to the larger size (d.d. 6.5 mm) of the type, the largest Marion Island specimen at d.d. 3.5 mm being slightly larger than Bernasconi's holotype of *Nullamphiura marionis*. The discrepancies in the published descriptions of the two nominal species, such as the contiguity of the adoral shields (said to be touching in *A. tomentosa* and separate in *N. marionis* – appearing abnormally so in the pair figured by Bernasconi in 1968) are attributable to variation. Indeed Bernasconi (1971) notes that the adorals are 'rarely joined'. The distinctive widely separated radial shields of larger specimens (d.d. 3 mm or more) agree with Bernasconi's and Lyman's descriptions (though in his figures they appear almost contiguous distally). There may also be naked patches of skin in some of the ventral interradii of the present Marion Island specimens as well as in the holotype of *A. tomentosa*. I think that the lack of imbrication in the disc scales of the latter is due to the somewhat distended condition of the disc. The shape of the oral shields is rather variable but they never have such a large proximal angle as in *Amphiura lymani* (Studer) from the vicinity of South Georgia, which is otherwise rather similar, lacking tentacle scales, as Bernasconi notes. Her supposed difference that *A. lymani* has smaller distal oral papillae than proximal (infradental) ones, whereas the reverse is the case in the Marion Island species, is not supported by the present specimens or the 'Discovery' material of *A. lymani* from South Georgia, of which Mortensen's figure (1936, fig. 14, p. 275) is misleading in showing the distal papillae as much smaller

than their true size which I reckon approximately equals the size of the infradental papillae. In the Marion Island specimens the distal papillae are variable not only in size but also in shape, being either pointed or rounded at the tip. The dorsal arm plates have their distal edges flattened medially in these Marion Island specimens and can better be described as fan-shaped than rhombic, as Bernasconi describes them. The ventral arm plates are pentagonal.

As for the generic position of this species, in 1970 I rejected *Nullamphiura* Fell on the grounds that the number of tentacle scales unsupported by other characters is inadequate for a generic distinction from *Amphiura*, being variable in several species and resulting in artificial grouping of otherwise morphologically diverse species (Clark, 1970). In fact, the holotype of *Amphiura tomentosa* does have a few pores showing a rudimentary scale, though these are quite lacking in the smaller Marion Island specimens.

It is surprising that *A. tomentosa* has not been reported again from Kerguelen despite extensive collections by the French and the B.A.N.Z.A.R. Expedition.

Ophiurolepis martensi (Studer)

Ophioglypha martensi Studer, 1885 : 161, pl. 2, fig. 8.

Ophiurolepis martensi : Mortensen, 1936 : 321-323, fig. 39.

MATERIAL. Z 55 (pt), in holdfasts of the giant kelp *Macrocystis pyrifera* ; 14 specimens.

All these shallow-water specimens as well as 57 others taken by the 'Discovery' Investigations off Marion Island in 88-113 m consistently have the disc plating irregular. In contrast, out of a total of 168 specimens from South Georgia - the type locality - no less than 109 or 65 % have a more or less regular rosette, as Mortensen's figure (1936) shows ; also of 91 specimens from McMurdo Sound in the Ross Sea, 70 % have regular discs. Possibly this difference is enough to justify a sub-specific distinction of the material from the vicinity of Marion Island but there is no obvious morphological difference between them and those specimens from other localities which share their irregular disc plating.

One of these specimens has a number of ? loricates in the grooves between the disc plates.

Ophiacantha vivipara Ljungman

See : Mortensen, 1936 : 246-248, pl. 7, fig. 2.

MATERIAL. Z 57, in the holdfasts of *Macrocystis* (rare) ; 5 adult specimens with several emerging and loose young.

This species was evidently not taken by the 1965/66 expedition, though collected by the 'Discovery' Investigations at 90 or more metres off Marion Island.

ASTEROIDEA

Anasterias rupicola (Verrill)

See: Bernasconi, 1971: 285, pl. 85, figs 1, 5.

MATERIAL. TVLT 14, among boulders at 3.5 m; 6 specimens.

LD 10, in depressions and crevices at LWS; 3 adults with 3 young.

GT 4, on a vertical face at 3 m; 2 specimens.

Z 3, in a rock pool at LWS; 1 specimen.

Z 31, in the pool connected to the sea by a tunnel; 2 specimens.

The largest one of these specimens has R 58–65 mm and exceeds any other record for the species, although one of Bernasconi's had R 49 mm.

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A NEW SPECIES OF *TILAPIA* (PISCES, CICHLIDAE) IN THE ZAMBIAN ZAÏRE SYSTEM

By ETHELWYNN TREWAVAS & DONALD J. STEWART

SYNOPSIS

A new species of the cichlid genus *Tilapia* A. Smith, 1840, is described from the Luongo River, a tributary of the Luapula in northern Zambia. It is assigned to the subgenus *Tilapia*. Compared to its near relative, *T. sparrmanii*, the new species is more elongate, with higher modal number of vertebrae (28, cf. 27) and a slightly longer caudal peduncle and has relatively shorter pectoral fins, features suggesting adaptation to flowing waters. The new species also appears to exhibit sexual dichromatism in the dorsal fin, an unusual feature in substrate-spawning *Tilapia*.

INTRODUCTION

THE new *Tilapia* described herein was collected by Dr Eugene K. Balon* while he was stationed at the Central Fisheries Research Institute (UNDP/FAO), Chilanga, Zambia, in 1970. Fish samples were taken in the Luongo River as part of Dr Balon's stock and production assessment programme for Lake Mweru and its drainage area. Analysis of the Luongo fish collections is continuing; a complete taxonomic and zoogeographic survey of the fish fauna will be published later.

The Luongo River is an eastern head-water stream of the Zaïre basin and enters the Luapula River about 20 km upstream from Johnston Falls. On the Luongo about 20 km upstream from its mouth Musonde Falls may have historically formed a barrier to upstream movement of some fish species. Recently a dam was built in the vicinity of Musonde Falls, completely isolating upstream areas. The new *Tilapia* was collected at two localities above Musonde Falls: (a) Nsenga (or Insenga) stream, a shallow, clear forest stream, 2–6 m wide with banks overgrown with brush, (b) Luongo River mainstream, a sluggish, turbid stream 18–20 m wide, 0.5–4 m deep, in open savannah with a deep, grassy ravine.

ABBREVIATIONS AND MEASUREMENTS

BMNH = British Museum (Natural History)

ROM = Royal Ontario Museum

SL = Standard length

The upper jaw is measured from the anterior point of the upper lip to the posterior end of the maxilla, the lower from the anterior point of the lower lip to the posterior end of the jaw, here the position of the retroarticular.

The preorbital bone is measured from the middle of its orbital rim along a line continuing the radius of the eye at that point.

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The last ray of the dorsal and anal fins is counted as one if it is separate from the penultimate at its base, even if it is smaller than the penultimate. A simple ray fused basally to the penultimate is not counted.

Tilapia baloni n. sp.

HOLOTYPE. ROM 28120: male, 136+30 mm, Nsenga stream, tributary of Upper Luongo.

PARATYPES. ROM 28120: 5 males, 86+23.5 to 114+28 mm, 6 females, 83+22 to 106+25.5 mm and a juvenile of 50+c, same field data as holotype.

ROM 28071: 3 males, 90+26.5 to 113+29.5 mm from Luongo River above Musonde Falls.

BMNH 1974.4.23.1: male, 138+36.5 mm from Luongo River above Musonde Falls (formerly ROM 28071).

BMNH 1974.4.23.2-4: female, 101+27 mm and 2 males, 100+26 and 85.5+22 mm from Nsenga stream (formerly ROM 28120).

DESCRIPTION. Meristic characters from holotype and all paratypes, proportions from holotype and 6 male and 5 female paratypes of 82.5-138 mm SL.

Proportions as % SL. Depth of body 36.5-41.7 (over 40.5 in only 2); length of head 30.4-32.0; length of pectoral fin 23.0-29.0 (over 28 in only 2); length of caudal peduncle 13.3-17.2, 14 or more in all but 1 specimen (0.96-1.25 times its depth, less than 1.0 in only 2 specimens).

Proportions as % length of head. Length of snout 33.9-38.4; diameter of eye 24.6-29.0; depth of preorbital 18.0-21.6; interorbital width 33.0-36.6; length of upper jaw 29.5-34.6, of lower jaw 35.5-38.5.

Maxillary not extending to below eye. Teeth in 3-5 rows in upper jaw, 3 or 4 in lower, 40-50 in outer row of upper jaw. Outer teeth bicuspid with the main cusp obliquely or rectangularly truncate; inner tricuspid with subequal cusps.

Gill-rakers on first arch (1-2)+1+(8-10, usually 8 or 9), short, those near the joint often bluntly bifid. Microbranchiospines present on outer sides of 2nd, 3rd and 4th arches.

Lower pharyngeal bone (Fig. 2) with a median length of 24.3-29.4% length of head, and width 31.4-36.3%, with short blade, 0.55-0.63 length of toothed area; teeth slender, the posterior bicuspid, the anterior kukri-shaped.

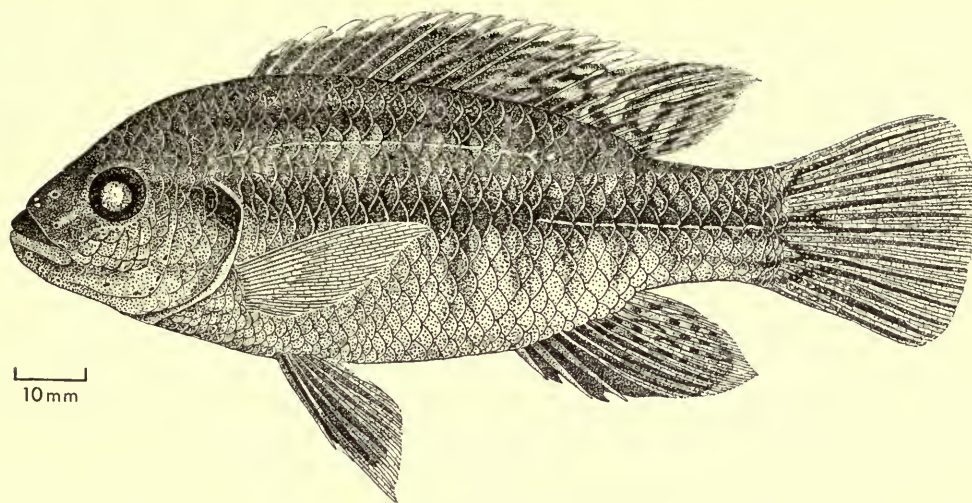
Scales on cheek in 3 horizontal rows; in lateral line series 29 or 30, between origin of dorsal and lateral line $3\frac{1}{2}$ or (usually) 4; around caudal peduncle 16. Circuli granular, mostly in a roman pattern but occasionally a few gothic.

Dorsal XIV 10 (f.2), XV 9 (f.1), XIV 11 (f.1), XV 10 (f.16) or XV 11 (f.2); last spine 14.5-17.8% SL, soft rays not greatly prolonged.

Anal III 9, third spine 14-15% SL.

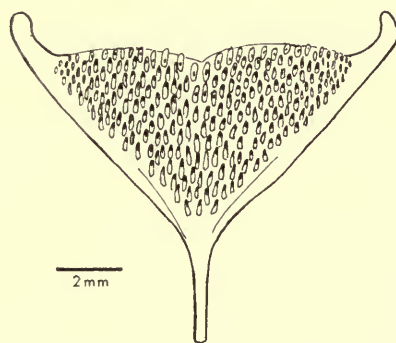
Pelvics not quite reaching vent. Caudal truncate with angular or rounded corners, scaly only at the base and not densely.

Vertebrae 27 (f.3), 28 (f.17) or 29 (f.1).

FIG. 1. *Tilapia baloni*, holotype.

Genital papilla of male conical or bluntly bifid, of female a short pigmented tube with scalloped rim. Loose ovarian eggs with long diameter about 1.9 mm in a fish of 100.5 mm.

Intestine in a specimen of SL 95 mm a little over 3 times SL, this and the stomach containing fine dark debris including parts of vascular plants, sparse fragments of filamentous algae and some desmids.

FIG. 2. Lower pharyngeal bone of *Tilapia baloni*, holotype.

Colour (from colour photographs taken by Dr Balon from recently killed fishes). Snout, top of head and dorsum dark blue-green, nearly black in adult male; flanks more diffuse green with 9 or 10 dark vertical bars and 2 horizontal bands present or absent (present in all preserved fish); scales of lower half of flanks and caudal peduncle each with a dark spot either centrally or at base. In the larger male main part of operculum and flanks around, below and behind pectoral crimson; fainter indications of same colour in other males.

Spinous dorsal dusky with vague paler spots and a submarginal black band ; soft dorsal proximally with spots or a dark reticulum with light interstices, distally with dark streaks between the rays ; a tilapia-mark on the dorsal fin in all specimens. In males dorsal lappets whitish with a pinkish tinge ; upper edge of soft dorsal and postero-dorsal corner of caudal the same colour. In females lappets dark or dusky, but soft dorsal and corner of caudal sometimes with narrow pale edge.

Anal dusky, with or without a pale tip. Pelvics dusky, pectoral transparent. Caudal with horizontal dark streaks between the rays.

T. baloni is so far known only from the Luongo River above Musonde Falls. A search through the British Museum and University of Michigan collections of *T. sparrmanii* from the Luapula basin and the Bangweulu Region revealed no overlooked specimens of the new species and none was encountered during the survey of the Kafue Flats in which one of us (D. J. S.) took part in 1969/70. We have both examined catches in the Mweru basin without finding it.

Dr Balon informs us that there is topographical and geological evidence that the upper Luongo once drained to the Kalungwishi, an eastern tributary of Lake Mweru. Some headwater streams of the Kalungwishi River rise in the swamps of the Kawambwe plateau, whose waters also feed the Luongo. The fish fauna of the upper Kalungwishi is not well known.

(The 'undescribed species from the Lake Mweru area' related to *T. sparrmanii* mentioned by Thys (1968 : 369) was *T. ruweti* and not *T. baloni*.)

AFFINITIES. *T. baloni* most resembles *T. sparrmanii* A. Smith, within whose general area of distribution it is found, but *T. baloni* is a more attenuate fish with a more acute head. The different shape of the body is expressed in the lower ratio of depth to length and the shape of the caudal peduncle as well as the number of vertebrae (Table 1). There is also a higher modal number of scales, but since this is true not only of the lateral line series but also the number between lateral line and origin of dorsal fin and rows on the cheek it may not be related to the presence of an additional metamere, the basic difference being the smaller size of the scales. The pectoral fin is usually relatively shorter, a feature which with the slender form probably indicates a stronger swimmer, with less use of the pectorals as paddles and balancers and more use of the tail for propulsion. At the sizes of our examples some individuals of *T. sparrmanii* have an additional row of teeth, but this is not constant. The long intestine and its contents in the one specimen examined do not suggest a sharp difference in feeding habits between this and *T. sparrmanii*. Duerre (1969) found a preponderance of periphyton in the diet of the latter in the upper Zambezi, with organic debris an important supplement.

The two species differ also in colour. In *T. sparrmanii* the red colour on the flanks takes the form of red edges to the otherwise green scales around and behind the pectoral. In the biggest photographed (male) *T. baloni* it is a red flush involving the greater part of the operculum and the abdominal region at and below the level of the pectoral nearly to the ventral surface. It is more metallic in appearance than the red of the flanks characteristic of most species assigned to subgenus *Coptodon*. In the latter and *T. sparrmanii* males and females are coloured alike in body and fins.

TABLE I

Contrasts between *T. baloni* (22 specimens, 1 of 50 mm, 21 of 82–136 mm in SL) and *T. sparrmanii* (proportions in 16 specimens 82–126 mm SL, meristic characters also in others) from the Luapula basin and Bangweulu region

	<i>T. sparrmanii</i>	<i>T. baloni</i>
Depth of body (% SL)	39.5–50.0 (only 2 < 41.5)	36.5–41.7 (only 2 > 40.5)
Length of pectoral (% SL)	24.0–32.5	23.0–29.0
23.0–27.9	f. 4	f. 20
28.0–29.0	2	2
29.1–32.5	10	0
Length of caudal peduncle (% SL)	12.0–15.3	13.3–17.2
divided by its depth	0.66–0.99	0.96–1.25 (only 2 < 1.0)
Scales : l.l. series 26	f. 2	f. 0
27	18	0
28	17	0
29	5	15½
30	2	6½
D-l.l. 3	f. 19	f. 0
3½	24	6
4	5	15
4½	1	1
cheek rows 2	f. 37	f. 0
3	7	22
Dorsal spines XIII	f. 2	f. 0
XIV	38	3
XV	9	19
Total dorsal rays 23	f. 1	0
24	11	3
25	30	17
26	7	2
Modal formula	XIV 11	XV 10
Vertebrae 26	f. 2	f. 0
27	22	3
28	8	17
29	0	1

T. ruweti (Poll & Thys van den Audenaerde) is also found on the Kawambwa plateau in waters including tributaries of the Luongo (specimens in Chilanga Fisheries Research Station, examined by E. T., others collected by Dr Balon examined by D. J. S.). Its modal dorsal formula is XIV 10, nearly approached by XIV 11, and the modal number of vertebrae, as in *T. sparrmanii*, is 27. Its caudal fin is rounded. It has not been recorded at sizes greater than 80 mm SL and is more slender than *T. baloni*, with an even shorter pectoral fin. Distinctive elements of the colour pattern are the tricolour band edging the dorsal fin and the light blue and purple-red spots on soft dorsal and caudal fins. No sexual dichromatism has been reported.

T. sparrmanii is present below Musonde Falls, but has not been caught in the Upper Luongo. *T. ruweti* is sympatric with *T. baloni* in the Upper Luongo, just as elsewhere (e.g. in the Mweru lagoons) it is caught together with *T. sparrmanii*.

The fact that to this extent *T. baloni* occupies the niche elsewhere belonging to *T. sparrmanii* suggests that it is either a vicariating species or a subspecies of the latter. We have no evidence so far that the differences are less than specific, and the probability that there are colour and size differences between the sexes in *T. baloni* is further support for its specific status. Although *T. sparrmanii* is reported from rivers, it is not a fish of the main streams, but occupies lagoons and backwaters rich in vegetation. *T. baloni* is probably derived from *T. sparrmanii* or a *sparrmanii*-like common ancestor in response to life in a river-bed of steeper gradient than that favourable to *T. sparrmanii*, with all that it means in terms of locomotion and food.

Sexual dichromatism in the dorsal fin of *T. baloni* is a significant difference between it and other species of *Tilapia* (as distinct from *Sarotherodon*) and it suggests that the sexes may differ more in their courtship roles than is usual in *Tilapia*.

We place the new species in subgenus *Tilapia*, which includes the two species with which we have compared it (as well as *T. guinasana* in the opinion of one of us, E. T.) because of the bicuspid pharyngeal teeth (tricuspid in most species of subgenus *Coptodon*), low total numbers of dorsal rays and the relatively narrow preorbital bone. But there are two features in which *T. baloni* resembles the species included in *Coptodon* – the modal number of vertebrae, also 28 in *Coptodon*, and the presence of 3 rows of scales on the cheek. The species, *T. (Coptodon) rendalli* Boulenger, that is found in the same geographical area as *T. baloni* and *T. sparrmanii* is the one most unlike these species, having a modal 29 vertebrae, and is more advanced in some other ways, and this is another reason for relating *T. baloni* to the species of *T. (Tilapia)*.

ACKNOWLEDGEMENTS

We have pleasure in recording our gratitude to the following: Dr Eugene K. Balon, University of Guelph, Ontario, who collected the species, for putting his notes and colour slides at our disposal; Drs W. B. Scott and E. J. Crossman, Royal Ontario Museum, Toronto, for making available material under their curatorial care; Dr R. M. Bailey, University of Michigan Museum of Zoology, Ann Arbor, Michigan, for providing D. J. S. with facilities for work on the Luongo River collections; the authorities of the British Museum (Natural History) for the facilities enjoyed by E. T. including the making of radiographs (by M. McLellan) for vertebral counts and use of the drawing by Sharon Chambers; Mr Graham Bell-Cross for introducing *T. ruweti* to E. T. in the Mweru basin in 1965.

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TWO NEW NEMATODES PARASITIC IN THE KIWI IN NEW ZEALAND

By EILEEN A. HARRIS

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SYNOPSIS

Two new species of nematodes, *Heterakis gracilicauda* sp. nov. and *Cyrnea (Cyrnea) apterycis* sp. nov., are described from the kiwi (*Apteryx* sp.) in New Zealand.

INTRODUCTION

THROUGH the kindness of Mr D. M. Rutherford of the Whangarei Animal Health Laboratory, Whangarei, South Island, New Zealand, a small collection of nematodes obtained from a kiwi (*Apteryx* sp.) was received for study. So far as the writer is aware, the only record of nematodes occurring in *Apteryx* appears to be that of Chatin (1884, 1885), who gave a very brief and inadequate description of a form that he called *Ascaris apterycis*. This species does not seem to have been met with again, and it is therefore not surprising that the present material has proved to be very interesting, consisting as it does of two new species which are described below.

DESCRIPTION OF SPECIES

Family **HETERAKIDAE** Railliet & Henry, 1914

Heterakis gracilicauda sp. nov.

(Figs 1 & 2)

DESCRIPTION. This description is based upon specimens from the caecum of *Apteryx* sp. in South Island, New Zealand.

The male measures 3.3–4.4 mm in length and 0.17–0.33 mm in maximum thickness and the female 5–6.4 mm and 0.19–0.3 mm, respectively. The head bears the usual three lips without interlabia, and no teeth have been made out (Fig. 1). The diameter of the head taken just at the base of the lips is approximately 42–49 μ m. There is a short pharynx measuring 30 μ m in length, and this leads into an oesophagus terminating inwardly in a distinct bulb, which measures

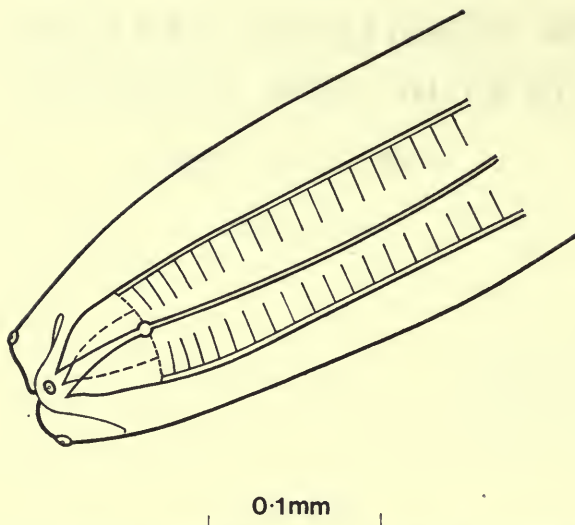


FIG. 1. *Heterakis gracilicauda* sp. nov.: lateral view of head.

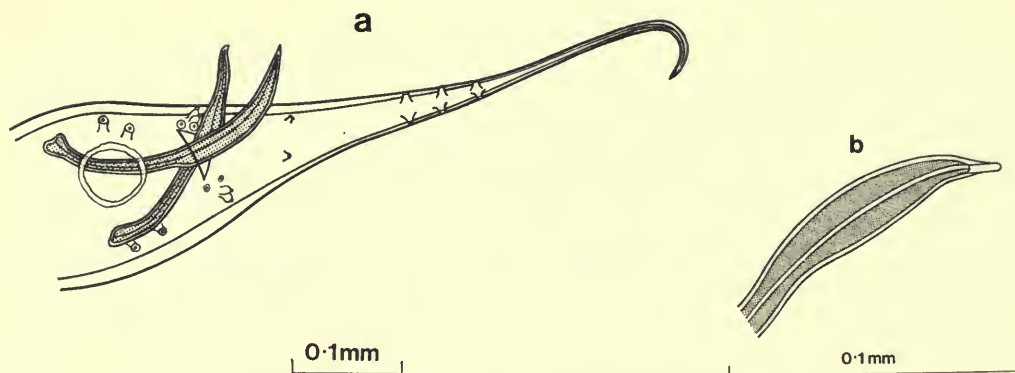


FIG. 2. *Heterakis gracilicauda* sp. nov.: (a) ventral view of male tail; (b) tip of spicule.

0.14–0.16 mm in length and 0.11–0.13 mm in width. The total length of the pharynx together with the oesophagus, including the bulb, is 0.52–0.7 mm in the male and 0.7–0.85 mm in the female. The nerve-ring is situated at approximately 0.17 mm from the anterior end of the body. The excretory pore occurs just posteriorly to the nerve-ring at 0.26 mm from the anterior end. No cervical papillae have been observed.

The caudal end of the male is long, slender and tapering, ending in a long, thin process. It measures 0.49–0.52 mm from the cloaca to the extreme tip of the tail. The caudal alae are narrow and little developed. The sucker is situated at 59–70 μ m from the cloaca, and has a well-defined, chitinous rim. It measures 48–52 μ m in diameter from the outside of the sucker rim. There appear to be ten pairs of

caudal papillae arranged as shown in Fig. 2a. These are disposed as two pairs of pedunculate papillae around the sucker, two pairs of sessile papillae lateral to the cloaca and two large pairs of pedunculate papillae lateral to these. The other four pairs are distributed along the tail, and it is just posterior to the hindmost pair that the tail begins to narrow gradually.

The spicules are short, alate and constantly subequal, measuring 0.24–0.29 mm for the left and 0.16–0.18 mm for the right. They have a granulated appearance, are narrow proximally, but expanded slightly in their distal regions. The left spicule is constantly longer than the right and each spicule bears a small process at the tip, as shown in Fig. 2b. The vulva is situated anteriorly to the middle of the body, at approximately 2 mm from the anterior end. This leads into a muscular vagina which runs posteriorly for a short distance before opening into the uterus. The eggs measure 58–60 μm $\times$ 30–35 μm .

MATERIAL. British Museum (Nat. Hist.) Reg. no. 1974 : 577–627 (syntypes).

DISCUSSION. Inglis, Schmidt & Kuntz (1971) have divided the genus *Heterakis* into species-groups, based upon the structure and the relative lengths of the spicules. The present species in having subequal alate spicules falls into their '*Heterakis gallinarum*' group. Of the species in this group, *H. gracilicauda* is most similar to *H. isolonche* Linstow, 1906, but differs from it in the length of the spicules, those of the new species being less than half the length of those reported for *H. isolonche*. The ratio of spicule-length : body-length in *H. isolonche* is 1 : 9 for the left spicule and 1 : 7 for the right, in *H. gracilicauda* it is 1 : 20 for the right spicule and 1 : 15 for the left. It appears that in all the male specimens of *H. gracilicauda* examined the left spicule is longer than the right. This is somewhat unusual, because in other members of the '*H. gallinarum*' group, the relationship of the left spicule to the right is reversed.

It is interesting to note that in the collections of the British Museum (Natural History) there are specimens of *H. gallinarum** and of *H. isolonche* from Australia and of *H. beramporia* from New Guinea. It would seem, therefore, that the '*H. gallinarum*' species-group as defined by Inglis, Schmidt & Kuntz is quite widespread in the Australasian region.

Family SPIRURIDAE Oerley, 1885

Cyrnea (*Cyrnea*) *apterycis* sp. nov.

(Figs 3, 4, 5 & 6 ; Pls 1 & 2)

DESCRIPTION. This description is based upon specimens from the gizzard of *Apteryx* sp. in South Island, New Zealand.

The body is cylindrical and the cuticle is provided with fine, transverse striations. The male measures 3.5–6.8 mm in length and 0.19–0.26 mm in maximum thickness, and the female 4.8–7.4 mm and 0.2 mm, respectively. The head has a diameter of 30–40 μm . The dorsal and ventral lips are well developed and rather deeply bilobed, each bearing a median process. Both the lobes of each lip carry two

papillae, a large one adjacent to a small one. The two lateral lips or 'pseudolips' carry at their bases the three pairs of teeth typical of the subgenus (*Cyrnea*) (Pls 1 & 2). A large papilla-like structure is visible on each of the lateral lips and posteriorly to this there is a small amphid.

The oesophagus is, as usual, in two parts, a short anterior portion and a longer posterior portion, the total length being 1.1–1.8 mm in the male and 1.6–2.3 mm in the female. The nerve-ring is situated anteriorly to the junction of the two oesophageal regions, at about 0.20–0.26 mm from the anterior end of the body. No cervical papillae have been observed. The features of the caudal end of the male are exceedingly difficult to make out, as the tail of each male specimen is, as so often happens in spiruroid nematodes, coiled in a tight, double spiral. Nevertheless, the caudal alae are wide and well developed, and the tail is covered over a wide area of its ventral surface with cuticular elevations, which are arranged in longitudinal rows, extending forward to a position just anteriorly to the beginning of the alae. There are eleven pairs of papillae, which are disposed in the manner usually found in the genus *Cyrnea*, and shown in Fig. 3. There are four pairs of large, pedunculated, pre-anal papillae, situated just laterally and anteriorly to the cloaca, and two

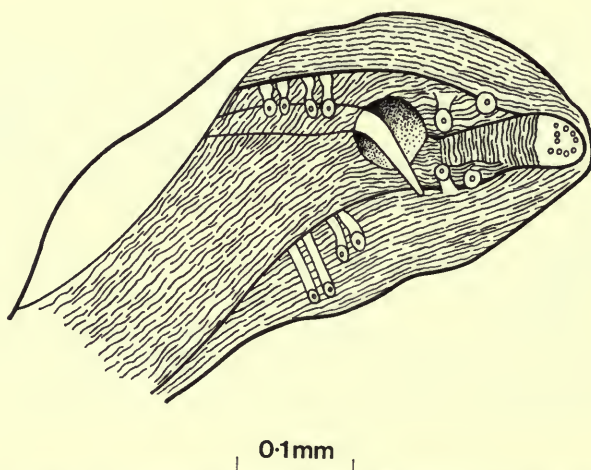


FIG. 3. *Cyrnea (Cyrnea) apterycis* sp. nov.: ventral view of male tail.

pairs posterior to the cloaca, whilst the remaining five pairs are very small and are distributed at the tip of the tail. They are arranged in two rows, each of four papillae, with the fifth pair lying centrally between the two rows. The spicules are unequal and dissimilar. The left spicule is long and slender, measuring 0.9–1.3 mm in length, and possesses a barbed tip (Fig. 4b). The right spicule is shorter and stouter, measuring only 0.18–0.25 mm in length and ends in a fine point. The proximal end is cup-shaped, as shown in Fig. 4a. In lateral view, the gubernaculum appears triangular in outline and measures 0.46–0.48 mm by 0.36–0.38 mm.

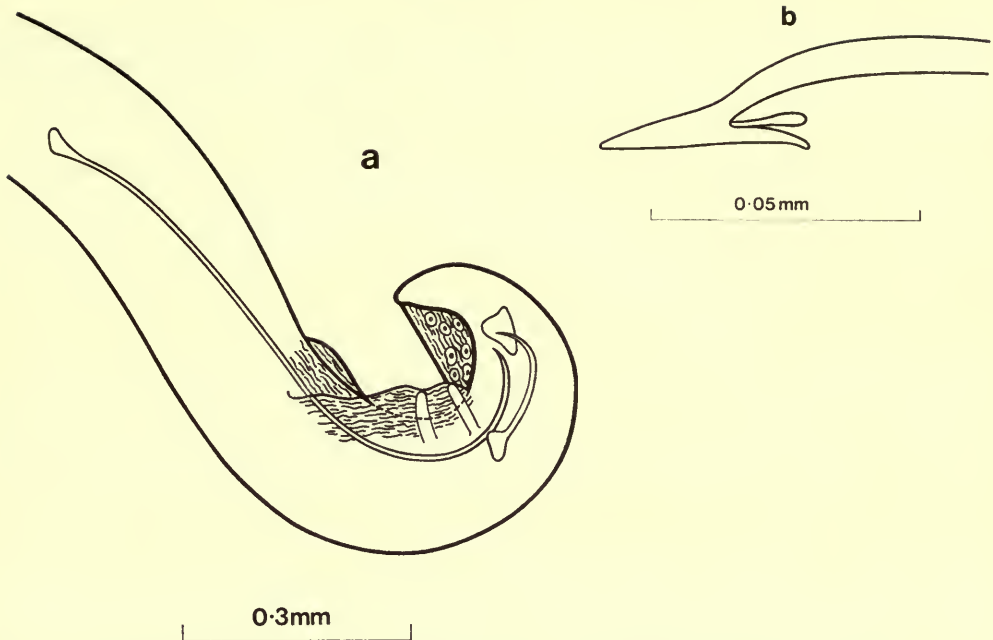


FIG. 4. *Cyrnea (Cyrnea) apterycis* sp. nov.: (a) lateral view of male tail; (b) tip of left spicule.

The tail of the female is conical and in some specimens it bears a small, flattened mucron at the tip (Fig. 5). The vulva is situated at 2.6–4.6 mm from the anterior end. From the vulva, the long muscular vagina runs backwardly to enter the

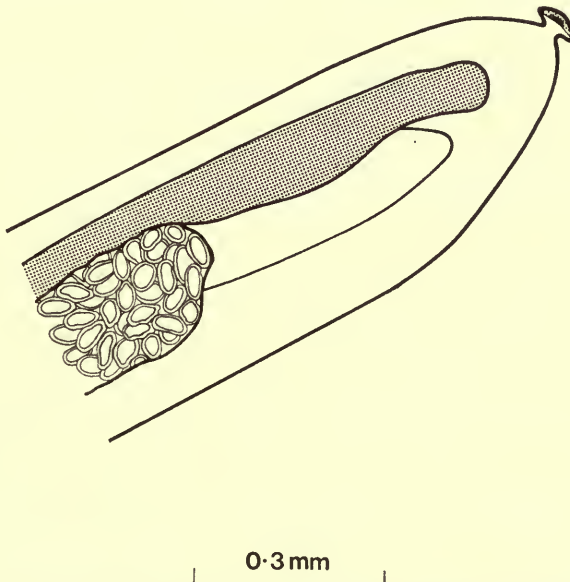


FIG. 5. *Cyrnea (Cyrnea) apterycis* sp. nov.: ventral view of female tail.

uterus, which bifurcates. One of the two uterine branches appears to run anteriorly for a short distance before bending posteriorly to run parallel with the other branch of the uterus (Fig. 6). The eggs measure 40–50 μm by 24–28 μm .

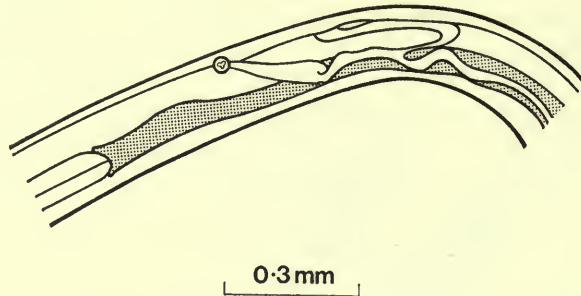


FIG. 6. *Cyrnea (Cyrnea) apterycis* sp. nov.: vulval region of female.

MATERIAL. British Museum (Nat. Hist.) Reg. no. 1974:628–667 (syntypes).

DISCUSSION. Chabaud (1958) has divided the genus *Cyrnea* into two subgenera, *Cyrnea (Cyrnea)* and *Cyrnea (Procyrnea)*. The position of the teeth on the 'pseudolips', situated deep in the buccal capsule, places the present specimens in the subgenus *Cyrnea (Cyrnea)*. In another work published later in the same year, Chabaud & Rousselot (1958) presented a differential key to the species of *Cyrnea (Cyrnea)*, and this key divided the subgenus into ten groups. In this key, the present specimens fall into their group 9, which includes *C. (C.) eurycerca* Seurat, 1914. This is regarded by these authors as the only valid species known hitherto in this group, for both *C. (C.) graphophasiani* Yamaguti, 1935, and *C. (C.) euplocami* Maplestone, 1930, are considered to be synonymous with *C. (C.) eurycerca*. *C. (C.) apterycis* differs from the latter species in having shorter spicules, and in the more anterior position of the vulva. It may also be distinguished by the number and distribution of the caudal papillae on the male tail. In *C. (C.) apterycis* there are six pairs of large, pedunculated papillae plus five pairs of small, sessile papillae, whilst in *C. (C.) eurycerca* there are only five pairs of large papillae, one pair of adanal and four pairs of small sessile papillae. The new species also possesses a barb-like tip to the left spicule.

Of the species described since Chabaud & Rousselot presented their key, only *C. (C.) ochotensis* Belogurov & Zueva, 1967, and *C. (C.) singhi* Ali, 1961, can be referred to the *C. (C.) eurycerca* group. *C. (C.) ochotensis*, described from *Falco subbuteo* in the U.S.S.R., differs from the present form in the greater length of its spicules. *C. (C.) singhi*, from *Centropus sinensis* in India, can be distinguished from *C. (C.) apterycis* by its much longer right spicule, by the number of cloacal papillae and by the apparent possession of only two pairs of teeth on the 'pseudolips'.

C. (C.) casuarii (Maplestone, 1932) has been placed by Chabaud and Rousselot in a separate group of its own. This species is mentioned here because it appears to be the only member of the subgenus to have been described hitherto from an Australian bird—*Casuarus biarunculus*. This nematode differs from the form

described above in its large size, being 4–7 times as long as *C. (C.) apterycis*, and in the number and arrangement of the caudal papillae of the male tail.

It is interesting to note that according to Mawson (1968), although *Cyrnea* spp. are fairly common in Australian birds, all have been determined as belonging to the subgenus *Cyrnea* (*Procyrnea*). She appears to have ignored *C. (C.) casuarii*, presumably because the host was resident in the Calcutta Zoo at the time of its death, but it is more probable that the infestation was a natural one rather than one acquired in India.

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PLATE I

Cyrnea (Cyrnea) apterycis – stereoscan micrographs of head

(a) Lateral view.

(b) Dorsal view.

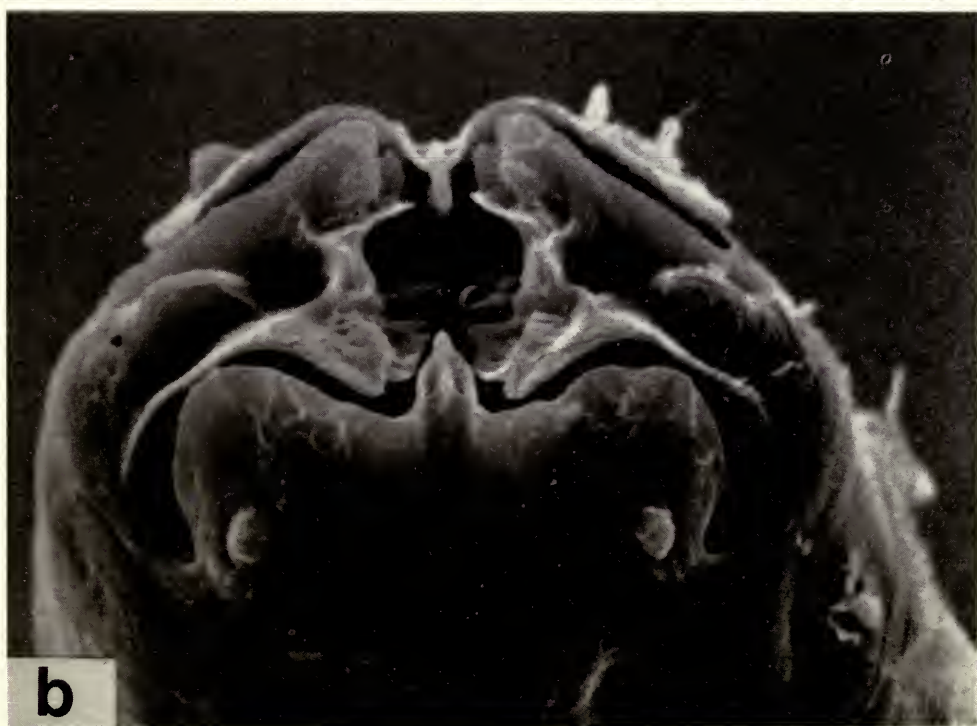
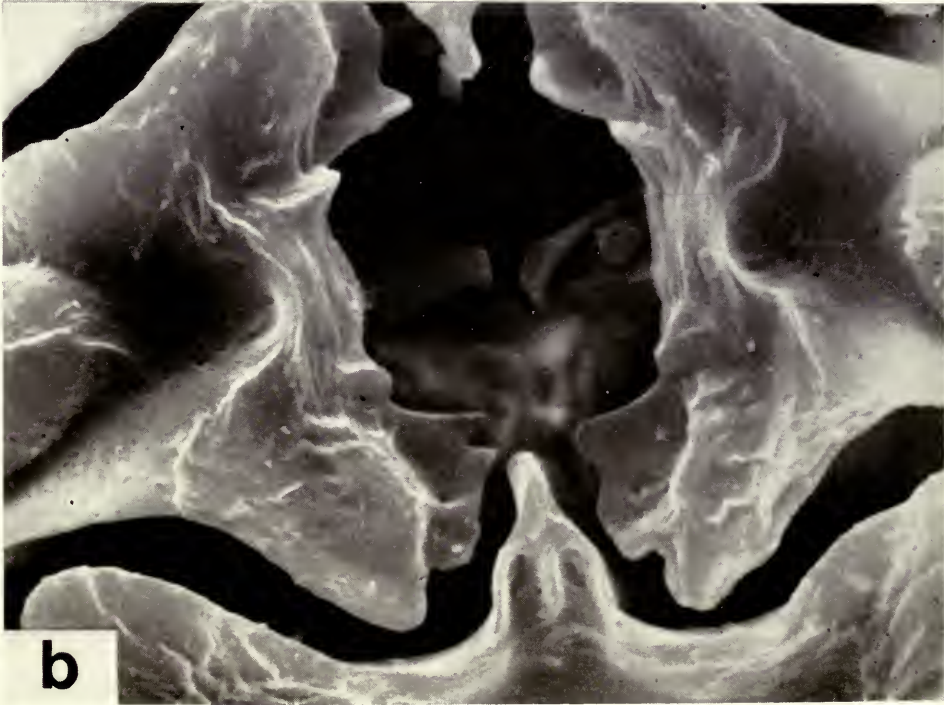


PLATE 2

Cyrnea (*Cyrnea*) *apterycis* – stereoscan micrographs of head

(a) En-face view.

(b) Teeth at base of 'pseudolips'.



DESCRIPTION OF *PEMBATOXON INSULARE* GEN. N., SP. N. FROM PEMBA ISLAND (MOLLUSCA PULMONATA, UROCYCLIDAE)

By JACKIE VAN GOETHEM

INTRODUCTION

FROM previous work on slugs of the family Urocyclidae, it appears that the lack of a stimulatory organ (*diverticulum atrii*, *stylophorus* or *sarcobelum*) in different species cannot be the peremptory argument for uniting them in a single genus. For example, in a recent revision of the group (Van Goethem, in press) it was clearly demonstrated that three species formerly united in a single genus, *Atoxon* Simroth 1888, could be divided into two groups on the basis of a wide variety of morphological characters. These groups have been recognized as separate genera; the first includes *Atoxon fasciatum* Verdcourt 1965, while the second is represented by *Atoxon meridionale* Forcart 1967 and *Atoxon bruggeni* Forcart 1967.

The specimens described below certainly represent a new species and though it lacks a stimulatory organ, it cannot be included in any described genus (e.g. *Atoxon*). A new taxon is, therefore, described here.

Abbreviations used in text : h. height ; M median tooth of radula ; lg. length ; w. width.

SYSTEMATICS

PEMBATOXON gen. n.*

TYPE SPECIES : *Pembatoxon insulare* sp. n.

DIAGNOSIS : Tail long and strong, with visceral cavity extending to its posterior end. Mantle posteriorly completely fused to the cephalopodium; covering an internal shell; mantle aperture present, forming a small, medio-dorsal slit at the posterior end of the mantle. Shell unguiform, presenting a more or less bilateral symmetry; nucleus at the posterior end, medially; protoconch oval. Jaw strongly arcuate, with a median projection on the ventral margin. Radula with median and laterals tricuspid; marginals lacking the endocone, bicuspid (some main marginals unicuspid, the ectocone being reduced or lacking), very slender, much longer than the laterals; mesocone of the marginals extending far beyond the posterior margin of the basal tooth plate. Pulmonary cavity little vascularized; heart transverse; aorta divided in two branches immediately after leaving the ventricle. Reproductive system: epiphallus with a small bursa calcifera and a long tubular caecum; hermaphrodite gland situated well behind the albumen gland, in the middle part of the tail; stimulatory organ absent; penis long, with

* *Pembatoxon* results from the contraction of *Pemba* and *Atoxon*.

a spiral torsion; penial sheath only near the proximal end separated from the penial tube; penial papilla simple, very small; praeputium very short; vagina absent; epiphallus 2, very short. Spermatophore helicoid, without an angle; presenting scaly spines over about its whole length; top blunt; filiform part very short. Alimentary tract forming 3 loops (intestine with one forwardly directed loop) and presenting a spiral torsion. Retractor muscles: the right upper tentacular retractor passes over the proximal end of the penis.

Pembatoxon insulare sp. n.

TYPE LOCALITY. Pemba Island, E. Africa.

GEOGRAPHICAL DISTRIBUTION. Only from the type locality.

MATERIAL. Pemba Island, E. Africa. Collected by C. Crossland, 1901. Material in British Museum (Natural History): holotype (Reg. No. 1909.5.10.52) and 5 paratypes (Reg. No. 1909.5.10.53-57).

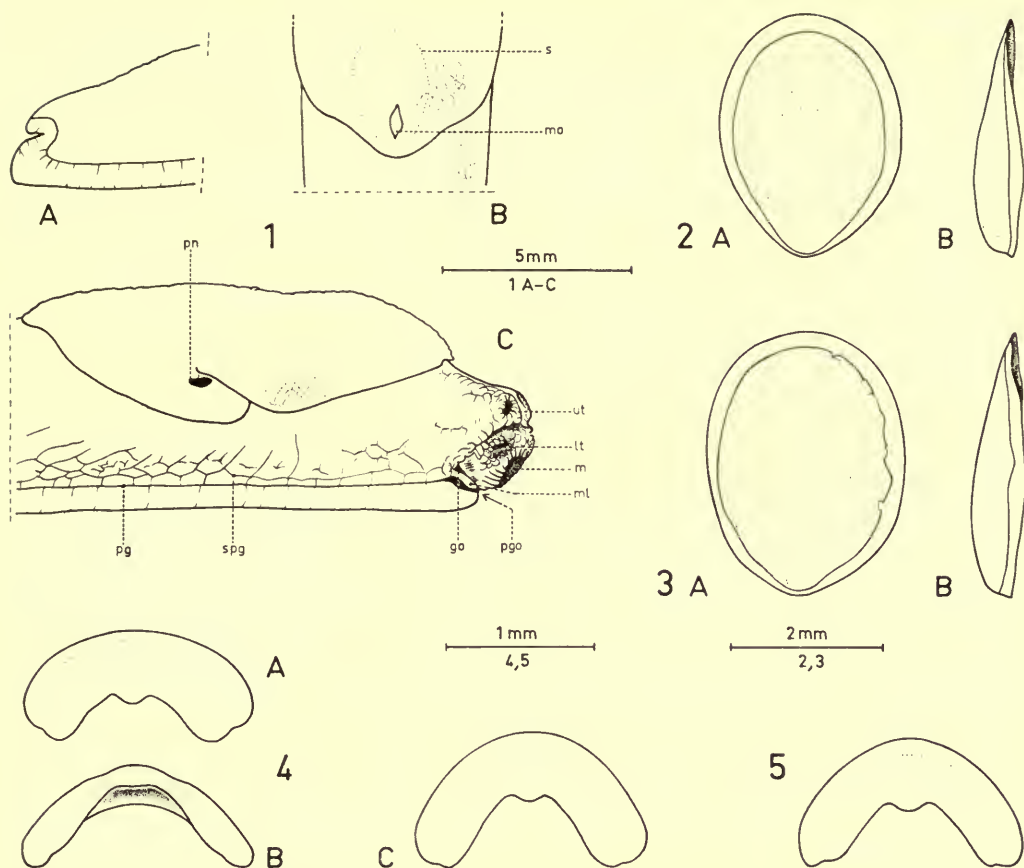
MEASUREMENTS. (in mm)

	Holotype	Paratype (1909.5.10.54)	Paratype (1909.5.10.55)
Body length	28.5	28.5	29.5
Body width at middle	5.5	6	6
Tail length	15	15.5	16.5
Mantle length	11.5	11.5	11.5
Mantle width at middle	9.5	10	10.5
Distance between respiratory orifice and anterior mantle margin	6.5	6.5	6.5
Length of respiratory orifice	0.5	0.7	0.5
Distance between respiratory orifice and posterior mantle margin	4.5	4.3	4.5
Height: maximum	6	6.5	6.5
at proximal end of tail	5	5.5	5.5
at posterior end of tail	2	2.5	2
Sole length	27	28.5	29
Sole width	2.8	3.5	3.5
Mid-area width of sole	1.0	1.2	1.2
Length of mantle aperture	0.8	0.7	0.8
Width of mantle aperture	0.4	0.2	0.2
Distance between mantle aperture and posterior mantle margin	0.7	0.6	0.8

DESCRIPTION.

External characters (Pl. 1, fig. 1-2; Fig. 1A-C)

Small slug with an adult length of c. 28 mm (in alcohol). Genital opening situated just behind and beneath the right lower tentacle, above the right anterior angle of the sole and just above the right mouth lobe. Tail long and well developed; its posterior end, at caudal gland level, slightly laterally compressed; not keeled; tapering backwards and ending in a well developed caudal horn (Fig. 1A); with fine longitudinal grooves (irregular on the dorsal part) limiting small polygonal tubercles and running to a fine irregular suprapedal groove. The latter being connected to the



FIGS 1-5. *Pembatoxon insulare* gen. n., sp. n.

Fig. 1. Holotype; A: Caudal end of the tail, lateral view; B: Posterior part of the mantle, dorsal view; C: Anterior part of the body, lateral view.

Fig. 2. Shell, holotype; A: Dorsal view; B: Lateral view.

Fig. 3. Shell, paratype 1909.5.10.53; A: Dorsal view; B: Lateral view.

Fig. 4. Jaw, holotype; A: Frontal view; B: Ventral view; C: Semi-frontal view.

Fig. 5. Jaw, paratype 1909.5.10.53, semi-frontal view.

(go, genital opening; lt, lower tentacle; m, mouth; ma, mantle aperture; ml, mouth lobe; pg, pedal groove; pgo, pedal gland opening; pn, pneumostome; s, shell; spg, suprapedal groove; ut, upper tentacle)

pedal groove by fine vertical grooves. Caudal aperture running to the posterior end of the sole. Mantle finely and very distinctly granulated. Mantle aperture small, slit like (Fig. 1B). Respiratory orifice, see Fig. 1C. Sole rather narrow. *Colour* (in alcohol): ground colour sandy; on the tail with a brown lateral stripe and a very fine, yellowish, medio-dorsal line (holotype); the ventral half of the tail, vaguely brown mottled. Posterior half of mantle with a trace of a brown lateral stripe. Sole unicoloured. Paratypes (1905.5.10.53, 56-57) sandy, unicoloured.

Shell (Figs 2-3)

Ovate, rather convex, concentrically striate, very thin, whitish. Nucleus raised, median, posterior, white. Periostracum pale yellow.

Holotype, lg. 3.2 mm; w. 2.4 mm; h. 0.6 mm.

Paratype (1909.5.10.53), lg. 3.5 mm; w. 2.6 mm; h. 0.7 mm.

Paratype (1909.5.10.55), lg. 3.6 mm; w. 2.8 mm; h. 0.7 mm.

Jaw (Figs 4-5)

Strongly arcuate, with a rounded median projection on the ventral margin.

Holotype, w. 1.6 mm; lg. 0.5 mm.

Paratype (1909.5.10.53), w. 1.5 mm; lg. 0.5 mm.

Paratype (1909.5.10.55), w. 1.7 mm; lg. 0.6 mm.

Radula (Figs 6-8)

Holotype (Fig. 6), formula: $(51+3+14+M+-) \times 124$. There is a rather distinct transition between laterals and marginals; only 3 transitional teeth; median tooth slightly asymmetrical. Median and laterals tricuspid. Marginals without endocones, very slender, with a high mesoconal supporting ridge; main marginals (teeth 25-40) very long, with generally a reduced ectocone (posterior margin of the basal tooth plate not reaching half the tooth length. Only c. 4 irregular teeth, with a blunt mesocone and several ectocones; generally 1 rudimental tooth. Size: 3.1×1.3 mm; c. 43 transversal rows/mm; length of M: 32-35 μ m.

Paratype (1909.5.10.53) (Fig. 7), formula: $(53+2+16+M+-) \times 130$. Endocone lacking from the 20th-21st tooth onwards. Most marginals between 20th and 42nd without an ectocone (unicuspid). Only c. 4 irregular teeth; generally 1 rudimental tooth. Size: 3.4×1.5 mm; c. 39 transversal rows/mm; length of M: 34-37 μ m.

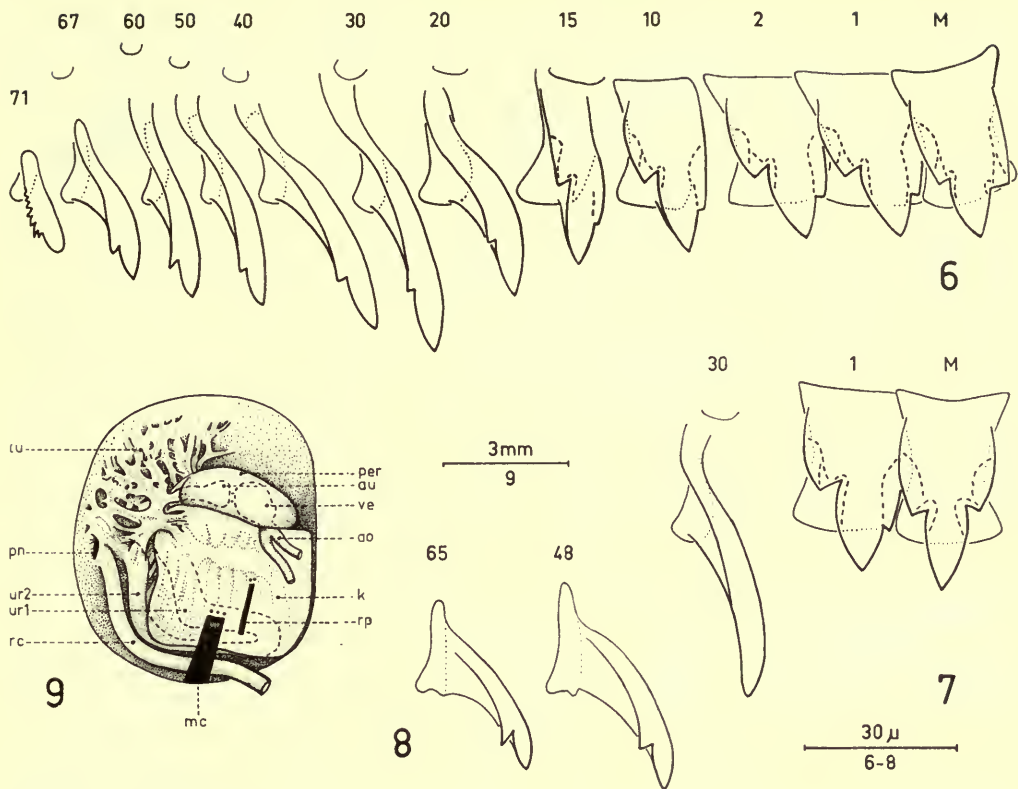
Paratype (1909.5.10.55) (Fig. 8), formula: $(60+3+16+M+-) \times 127$. Endocone lacking from the 22nd-23rd tooth onwards. Most marginals between 27th and 43rd without an ectocone (unicuspid). Mesoconal supporting ridge of marginals illustrated in Fig. 8. Only 4-5 irregular teeth; generally 1 rudimental tooth. Size: 3.3×1.5 mm; c. 39 transversal rows/mm; length of M: 34-37 μ m.

Pallial organs (Fig. 9)

Pulmonary cavity little vascularized. Kidney quadrangular. Heart transverse. Aorta divided into two branches immediately after leaving the ventricle; the anterior branch curving round the anterior loop of the intestine.

Reproductive system (Figs 10-13)

Holotype (Figs 10A-C, 11): Hermaphrodite gland (*ovotestis*) yellowish white, long and slender, with a weak torsion, situated in the middle part of the tail. Hermaphrodite duct (*ductus hermaphroditicus*) rather long, convoluted proximally. Albumen gland (*glandula albuminalis*) strongly developed, its middle part situated on a level with the posterior mantle margin. Common duct (*spermoviductus*) short,



FIGS 6-9. *Pembatoxon insulare* gen. n., sp. n.

Fig. 6. Radula, holotype.

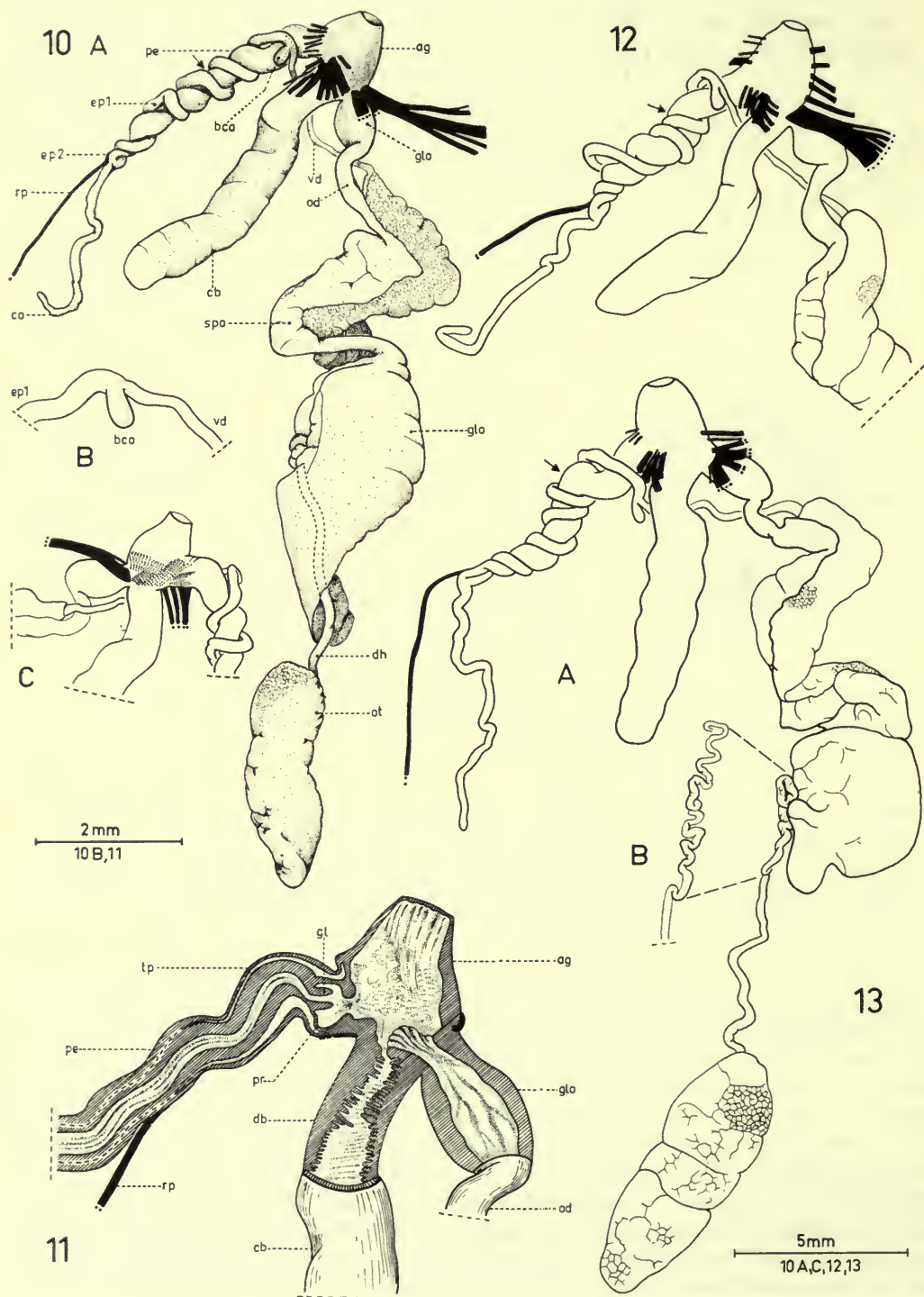
Fig. 7. Radula, paratype 1909.5.10.53.

Fig. 8. Two marginal teeth in almost lateral view, paratype 1909.5.10.55.

Fig. 9. Pallial organs, ventral view, holotype.

(ao, aorta; au, auricle; k, kidney; lu, lung (roof of pulmonary cavity); mc, columellar retractor muscle; per, pericardium; pn, pneumostome; rc, rectum; rp, penial retractor muscle; ur 1, primary ureter; ur 2, secondary ureter; ve, ventricle)

voluminous. *Vas deferens* short, passing under the spermathecal duct. Epiphallus with a small, ovoid *bursa calcifera* (Fig. 10B) at its distal end, and a tubular *caecum* (6.2 mm long) near its proximal end. Epiphallus 1, 12.5 mm long, wound around the penis and epiphallus 2 over its whole length. The latter very short (1.2 mm). Penis tubular, thick-walled, spirally torsive, clearly thicker than the epiphallus. Penial sheath (*tunica penis*) individualized at the proximal part of the penis (Fig. 11). Prepuce (*praeputium*) very short, separated from the genital atrium by a thick ring-wall. Penial papilla (*glans penis*) simple, very small (c. 0.25 mm long). Penial retractor muscle (*retractor penis*) very thin, long, arising from the left side of the diaphragm near the posterior margin of the kidney (Fig. 9), slightly adhered to the inner side of the penis windings and ending at about the distal end of the penial sheath (Fig. 10A, indicated by a small arrow; Fig. 11). Oviduct (*oviductus*)



very short. Oviduct gland (*glandula oviductus*) ovoid, with 4-5 rounded, well-developed irregular folds. Spermatheca (*bursa copulatrix*) consisting of a long, slender sac (*corpus bursae*), and a short, wide duct (*ductus bursae*), internally with numerous high, narrow folds; containing 2 spermatophores. *In situ*, the end of the spermathecal sac situated ventrally, on the same level as the insertion of the columellar retractor muscle. Atrium (*atrium genitale*) well developed, with numerous retractor muscles: at the issue of the oviduct gland, 3 long and strong ventral retractor bundles inserting at the left side of the foot-sole (on a level with the lung) and at the ventral side of the left body wall; at the issue of the penis and between penis and spermatheca several retractor muscles inserting at the right body wall. The ventral side of the atrium shows strong muscles (Fig. 10C, stipplings).

Paratype (1909.5.10.53) (Fig. 13A-B): Albumen gland quadrangular with a terminal lobe on the left side. Vas deferens wider at its distal end. The first section of the epiphallus, 14.5 mm long. Caecum, 9.0 mm long. Penis: distal end of penial sheath (indicated by a small arrow, Fig. 13A) is coincident with the insertion point of penial retractor muscle. Penial papilla very small, smaller than in the holotype, very near to the penial opening. Spermatheca containing a spermatophore.

Paratype (1909.5.10.55) (Fig. 12): Vas deferens a little wider at its distal end. The first section of the epiphallus, 13.5 mm long. Caecum, 8.0 mm long. Penis: distal end of penial sheath and insertion point of penial retractor muscle indicated by a small arrow on Fig. 12. Penial papilla not distinct; however, a small lobe can possibly be interpreted as a penial papilla.

Spermatophore (Pl. I, figs 3-4; Fig. 14A-I)

Holotype (Fig. 14A-I): Helicoid, with 6 windings. Length: *c.* 16.5 mm. Apex blunt, rounded. Only the apical part of the spermatophore (for nearly 1 mm) smooth. Outer side of the whorls with 4-5 irregular rows of forwardly directed scaly spines, each spine about 0.1 mm long. Posteriorly the number of rows decreases. Filiform section of the spermatophore, very short (*c.* 1.4 mm), with 1 sharp ridge (Fig. 14A, H) and 1 row of forwardly directed denticles (Fig. 14A, G, I), each denticle about 80-90 μ m long. Terminal opening present. A

FIGS 10-13. *Pembatoxon insulare* gen. n., sp. n.

Genitalia. Fig. 10. Holotype; A: General view; B: Detail of *bursa calcifera*; C: Ventral view of atrium and adjacent organs.

Fig. 11. Holotype, longitudinal section of atrium and adjacent organs.

Fig. 12. Paratype 1909.5.10.53.

Fig. 13. Paratype 1909.5.10.53: A: General view; B: Detail proximal part of hermaphrodite duct, partly unrolled.

(ag, *atrium genitale* (genital atrium); bca, *bursa calcifera*; ca, *caecum*; cb, *corpus bursae* (spermathecal sac); db, *ductus bursae* (spermathecal duct); dh, *ductus hermaphroditicus* (hermaphrodite duct); ep 1,2, *epiphallus* 1,2; gl, *glans penis* (penial papilla); gla, *glandula albuminalis* (albumen gland); glo, *glandula oviductus* (oviduct gland); od, *oviductus* (oviduct); ot, *ovotestis* (hermaphrodite gland); pe, penis; pr, *praeputium* (prepuce); rp, *retractor penis* (penial retractor muscle); spo, *spermoviductus* (common duct); tp, *tunica penis* (penial sheath); vd, *vas deferens*).

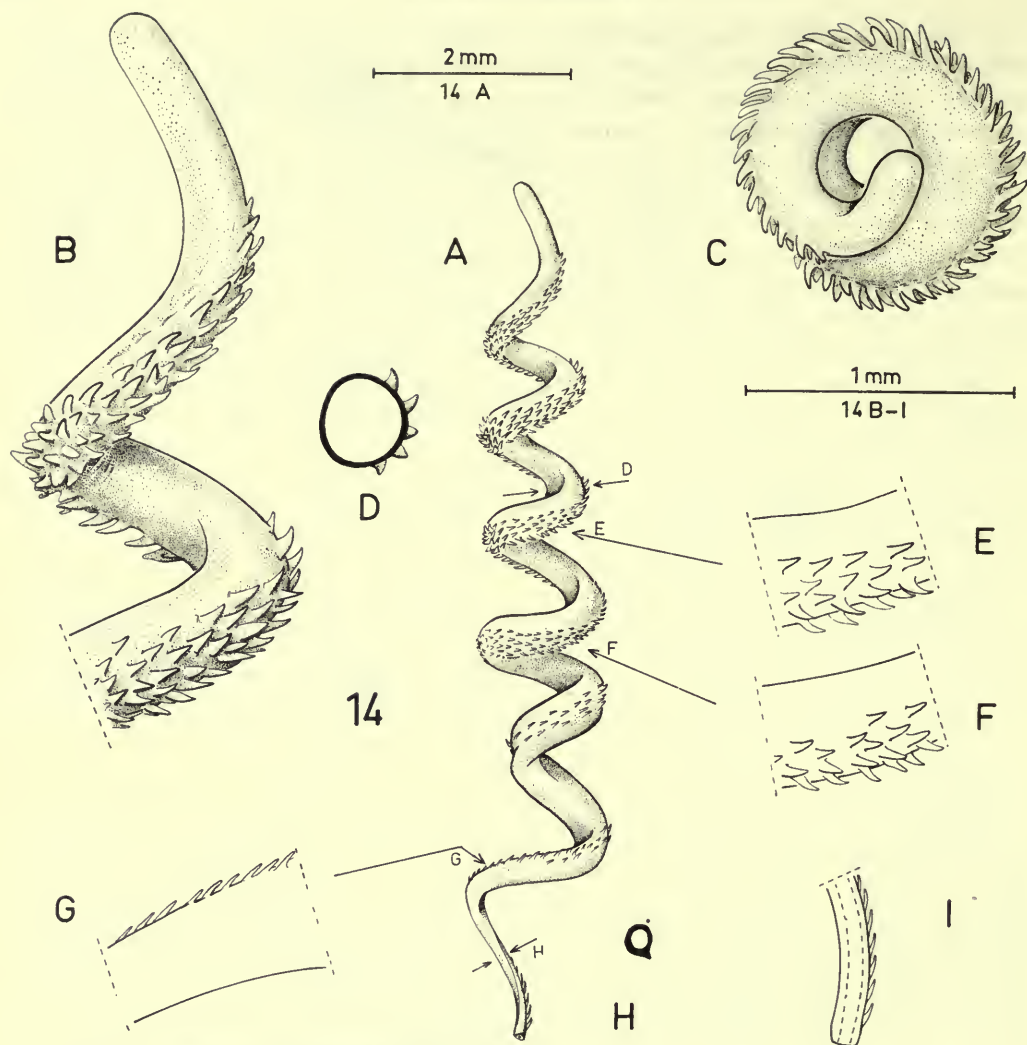


FIG. 14A-I. *Pembatoxon insulare* gen. n., sp. n.

Spermatophore, holotype. A: General view; B: Detail apical part, lateral view; C: Detail apical part, dorsal view; D: Transversal section at D in Fig. 14A; E: Detail of spines at E in Fig. 14A; F: Detail of spines at F in Fig. 14A; G: Detail of denticles at G in Fig. 14A; H: Transversal section at H in Fig. 14A; I: Detail terminal end.

second spermatophore, with the median area partially digested, measures *c.* 16 mm in length (the filiform part being *c.* 1.4 mm).

Paratype (1909.5.10.53) (Pl. 1, figs 3-4): Length: *c.* 16 mm (the filiform part measuring *c.* 1.5 mm).

Visceral organs

Visceral cavity extending to the posterior end of the tail. Alimentary tract forming 3 loops (intestine with one forwardly directed loop), presenting together

nearly a complete circumvolution. Posterior tip of the hermaphrodite gland extending behind the first loop of the alimentary tract. Anterior tip of the digestive gland extending to the inner side of the forwardly directed intestinal loop. Rectum passing above the basal part of the columellar retractor muscle (Fig. 9, ventral view).

Retractor muscles

The right upper tentacular retractor passes over the proximal end of the penis. Retractor muscles of the genitalia, see above.

DISTINGUISHING FEATURES OF THE GENUS AND SPECIES

Pembatoxon gen. n. resembles the genus *Atoxon* Simroth, 1888, in the absence of a stimulatory organ, but differs from that genus in :

1. the spermatophore having a very short filiform section ; a blunt, rounded apex and numerous forwardly directed spines over almost the whole length of the fusiform part ;
2. the penis having a short penial sheath and a very small penial papilla ;
3. the atrium having retractor muscles inserting at the left side of the foot-sole and at the ventral side of the left body wall ;
4. the absence of a vagina ;
5. the radula with relatively smaller number of laterals in comparison with the number of marginals.

Pembatoxon insulare gen. n., sp. n. differs from *Atoxon fasciatum* Verdcourt, 1965 (classified in a new genus, see J. Van Goethem in press) in :

1. the form of the spermatophore (see above) ;
2. the penis with a spiral torsion ;
3. the very short epiphallus 2 ;
4. the absence of a vagina ;
5. the aorta divided in two branches immediately after leaving the ventricle ;
6. the radula, with median and laterals not having a very long mesocone.

Pembatoxon insulare gen. n., sp. n. differs from *Atoxon meridionale* Forcart, 1967, and *Atoxon bruggeni* Forcart, 1967 (both species classified in a new genus, see J. Van Goethem, 1973) in :

1. the form of the spermatophore (see above) ;
2. the penis with a very small, simple penial papilla ;
3. the absence of a vagina ;
4. the radula with most of the marginals bicuspid ;
5. the right upper tentacular retractor passing over the proximal end of the penis.

ACKNOWLEDGEMENTS

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History) for the loan of the specimens and to the 'Komitee voor Elektronenmikroskopie van de vaste stof, Katholieke Universiteit Leuven' for enabling me to make the photographs of the spermatophore (Pl. 1, figs 3-4).

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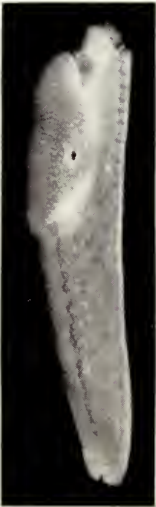
PLATE I

Pembatoxon insulare gen. n., sp. n.

- FIG. 1. Holotype, lateral view, $\times 2.1$.
FIG. 2. Holotype, dorsal view, $\times 2.1$.
FIG. 3. Spermatophore 1909.5.10.53 (Cambridge Stereoscan), fragment of third winding, $\times 125$.
FIG. 4. Spermatophore 1909.5.10.53 (Cambridge Stereoscan), denticles on one row, just before the filiform part, $\times 440$.



3



1



2



4



A QUAGGA, *EQUUS QUAGGA* (MAMMALIA, EQUIDAE), AT UNIVERSITY COLLEGE, LONDON AND A NOTE ON A SUPPOSED QUAGGA IN THE CITY MUSEUM, BRISTOL

By A. W. GENTRY

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A SUPPOSED QUAGGA SKULL IN THE CITY MUSEUM, BRISTOL	224
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SYNOPSIS

A mounted equid skeleton in the Department of Zoology, University College, London, is identified by its skull characters as *Equus quagga*, the extinct quagga of South Africa. An equid skull in the City Museum, Bristol, is not a quagga although accessioned as one.

INTRODUCTION

In the summer of 1972 I was asked to identify a mounted equid skeleton, Z581, in the museum of the Department of Zoology, University College, London. No written information existed about its history, but the number 41 had been written on the mandible a long time ago, and the late Professor D. M. S. Watson had once informed Dr K. A. Kermack that it was a quagga.

Z581 lacks canines and is therefore a female. It is adult ; all the permanent cheek teeth are in wear and their occlusal surfaces much flattened. Infundibula, otherwise known as marks or central cavities, are still present in the upper and first lower incisors, so that the animal could have been 10–15 years old, were its ageing at all comparable with that of horses. Upper first premolars are present on both sides.

Z581 is not a horse, hemione or ass. Horse is ruled out by the relatively great width of the skull across the zygomatic arch compared with that across the orbits, the rather squared outline of the occipital in rear view, insufficient narrowing of the more dorsal part of the premaxilla, and deep V-shaped internal sulci of the lower molars. The zygomatic width and the normal instead of diminutive size of the occipital rule out the hemione. It cannot be an ass because of the great zygomatic width, insufficient narrowing of the premaxilla, the lack of any marked backward deflection of the top of the occipital in side-view, and the curved rather than the

flattened lateral walls between the styles of the upper molars. There is no doubt that Z581 is a zebra, of which four species are known :

Grevy's zebra, *Equus grevyi* Oustalet, 1882, of parts of Somalia, eastern and southern Ethiopia and northern Kenya.

Mountain zebra, *E. zebra* Linnaeus, 1758, of the coastal region of the Cape Province of South Africa and southern South West Africa.

Burchell's zebra, *E. burchelli* Gray, 1824, with a range extending from the southern parts of the Sudan, Ethiopia and Somalia southwards to the Orange Free State and northernmost Cape Province.

Quagga, *E. quagga* Gmelin, 1788, an incompletely striped zebra formerly found in South Africa to the south of the Vaal River, in the Orange Free State and the southern Cape Province. It was heavily slaughtered in the 1850s and 1860s and became extinct in the 1870s. Specimens in European zoos survived until 1872 (London), 1875 (Berlin) and 12 August 1883 (Amsterdam). A number of specimens are available in museums, mostly as mounted skins, together with about a dozen skulls and five skeletons (Ridgeway, 1909; Hilzheimer, 1912; Rzasnicki, 1949; Lundholm, 1951; Willoughby, 1966; Rau, 1974).

COMPARISONS

The skull of Z581 was kindly lent to me for further study at the British Museum (Natural History). I established that it could not be a Grevy's zebra because it was too small, its face was short, and the premaxilla did not narrow in its upper parts. I then made a detailed comparison with up to 55 adult skulls of Burchell's zebra, 10 of mountain zebra and the museum's single example of a quagga skull, 1864.7.2.3, this last being from a complete skeleton of a male animal that lived in the London Zoo from 1858 until 1864 (Sclater, 1901). Its tooth wear is similar to Z581. The results of the comparison will be discussed character by character. The positions of all characters except the first are shown on a quagga skull in Fig. 1 and the skull of Z581 is illustrated in Plates 1-4.

1. The skull is smaller than in *Equus zebra*. Many *E. burchelli* approach it more closely, while the *E. quagga* skull is about the same size. It should be remembered that the quagga is a zoo specimen, that in the hemione and wild ass zoo specimens have skulls with linear measurements up to 10% smaller than their wild counterparts (Groves, 1966), that the same may be expected for zebras, and that Z581 may have been a zoo specimen itself. Thus the size of Z581 is appropriate for either *burchelli* or *quagga*. The back of M³ is more posterior relative to the front of the orbit in Z581 and the *quagga* skull than in *zebra*, while *burchelli* is intermediate. Hence *E. quagga* and Z581 are rather short faced, but this character appears to be linked with overall skull size in living equids, and both the large Grevy's zebra and large domestic horses have long faces.

2. The interorbital area of the frontals shows a slight doming in *burchelli* but is flatter in *zebra*. The *quagga* skull and Z581 both resemble *zebra*. There is a

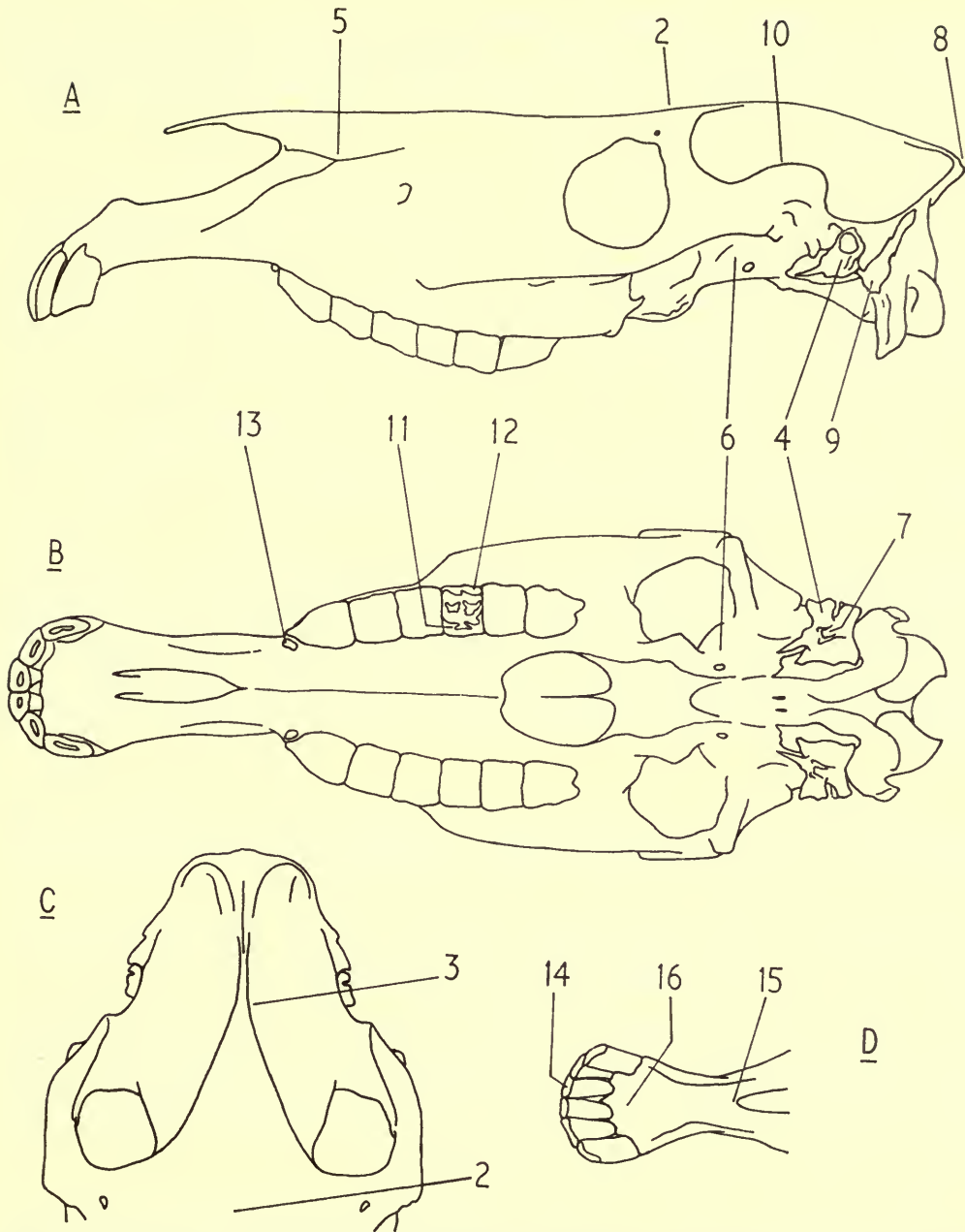


FIG. 1. Diagrams of a quagga skull to show the positions of characters 2 to 16, discussed in the text.

- A. Lateral view.
- B. Palatal view.
- C. Dorsal view of postorbital part of skull.
- D. Dorsal view of front of mandible.

possibility of regional variation within *burchelli* in that the doming seems less marked in specimens from South West Africa. Furthermore Dr D. A. Hooijer has told me that the *quagga* skull in the Leiden Museum shows a frontals' profile like *burchelli*. Nevertheless, Z581 would still lie beyond the *burchelli* range for the character, so that its affinities are with *quagga* or *zebra*.

3. The level of fusion of the two temporal lines to form a median sagittal line is more anterior in *burchelli* than in *zebra*. In 36 out of 50 *burchelli* it was forward of the rearmost level of the zygomatic arch in dorsal view; in the remainder it was level or behind. In 2 *zebra* it was anterior, and in 8 level or behind. The *quagga* skull and Z581 have the fusion in the more posterior position, thus being unlike most *burchelli* but not unlike *zebra*.

4. The external auditory meatus is slanted upwards as it passes laterally in *burchelli* but emerges horizontally in *zebra* in which most individuals also have a larger meatal orifice. Both Z581 and the *quagga* skull resemble *burchelli*.

5. The maxilla-nasal suture dips anteriorly as it approaches the top of the premaxilla in both *zebra* and *burchelli*, but the phenomenon is more pronounced in *zebra* in which the top of the premaxilla suture is also more rounded so that a flange of the nasal bone descends a short way behind the premaxilla. Unfortunately the sutures become obliterated in older individuals. They are no longer visible with complete certainty in the *quagga* skull, but in Z581 they resemble the *burchelli* pattern.

6. The alisphenoid area on either side of the basisphenoid antero-medially to the articulation for the lower jaw is more nearly horizontal in ventral view in *zebra* than in *burchelli*. Z581 and the *quagga* skull are like *burchelli*.

7. *E. zebra* has a longer styloid process between the auditory bulla and the meatus than does *burchelli*. Z581 is like *burchelli* and the *quagga* like *zebra*.

8. In side-view the top of the occipital is drawn out posteriorly in *zebra*, but not nearly so much in Z581 or the *quagga*. Among the sample of *burchelli* 17 resemble *zebra*, 17 resemble Z581 and *quagga*, while 15 are intermediate and indeterminate. This character can also be seen in rear view as a relatively high occipital in *zebra* and a relatively low occipital in Z581 and the *quagga*.

9. The mastoid bone is wider in *zebra* than in Z581 or the *quagga* skull. In *burchelli* it is narrow in 37 and wide in 18 skulls. The flange of the squamosal between the mastoid and the external auditory meatus is also sometimes wide and sometimes slim, but may well be associated with the mastoid width. Of the 37 *burchelli* with narrow mastoids only 11 also have a slender squamosal flange, but among the 18 with wide mastoids 11 is again the number with a slender squamosal.

10. In *zebra*, the top edge of the zygomatic arch is fairly straight in lateral view and remains at more or less the same level. In the *quagga* and Z581 the top edge is more strongly curved and ascends posteriorly. Of the *burchelli* sample 27 skulls are like *zebra* and 25 like *quagga*.

11. On the upper molars the protocone or inner pillar is elongated anteriorly in 40 out of 50 *burchelli* individuals but not in *zebra*. The *quagga* skull and Z581 both resemble the majority of *burchelli*.

12. Cement is better developed around the exposed sides of the cheek teeth of *zebra* than of *burchelli*. A crude assessment of 'more' or 'less' cement showed that in only 9 among 48 *burchelli* skulls was there as much cement as in 7 out of 10 *zebra*. Both the *quagga* and Z581 skulls had 'more' cement and can be considered to be more like *zebra* than *burchelli*.

13. A small P¹ is present in 5 out of 10 *zebra*, these being mostly the younger individuals. It is present on at least one side in 30 of 51 *burchelli*, is often larger than in *zebra*, and there are indications that it is less frequent among the older individuals; it also seems to occur less often in *burchelli* from South West Africa. Erz (1964) believes that the tooth is part of the deciduous dentition. When present in *burchelli* it is often accompanied by a concavity in the front part of the medial wall of P². A relatively large deciduous P¹ is present in Z581, with only a slight concavity on P², but it is absent on the *quagga* skull. For this character Z581 thus resembles *burchelli* and differs from *quagga*, but the character must be very unimportant for classification.

14. Infundibula, marks or central cavities, are present in the lower incisors of *zebra* although less marked than those appearing in the uppers. This condition agrees with horses (Grossman, 1953:400). In old individuals the infundibula disappear from upper and lower incisors. However in *burchelli* infundibula were present in the lower incisors of only 6 among the 42 individuals in which they occurred in the upper incisors, and in 2 of the 6 they were present in I₁s alone. The London sample of *burchelli* again gives a hint of regional variation in that those from South West Africa appear to have lower incisor infundibula more frequently. In Z581 and the *quagga* skull infundibula were present in the upper incisors and I₁. This intermediate state may best be counted as a difference from both *zebra* and *burchelli*.

15. The posterior edge of the mandibular symphysis in the median line is high and more or less upright in *burchelli*. In *zebra* the top edge dips gently as it passes backwards and so curves round at a lower level to become the posterior edge. The height of the posterior edge is thus less than in *burchelli*. This character is difficult to assess except in sectioned mandibles, but is real enough as can be seen from Lundholm's illustration (1951, fig. 2). Both the *quagga* skull and Z581 resemble *burchelli*.

16. The top surface of the mandibular symphysis is noticeably flat behind the incisors in both the *quagga* skull and Z581. It could be linked with the incisors' occlusal surface appearing to be very little upturned. This character contrasts with most *burchelli* and *zebra*, even when the latter have very well worn teeth. It does not appear to be linked with a regression of bone around the incisor roots such as has taken place in both the *quagga* skull and Z581.

DISCUSSION

It seems from the 16 characters considered above that Z581 can be taken quite safely as *E. quagga*. The characters can be summarized as in Table 1, from which it is seen that Z581 differs from *zebra* in 13 of the 16 characters, from *burchelli* in 5 of the 16, but from *quagga* in only 2 of 15 characters, one of the two being the scarcely significant presence of P¹s. Accepting Z581 as *quagga*, one can suggest that skulls of *quagga* are like *burchelli* but differ in flatter frontals, a shorter united sagittal line on the cranial roof, more cement around the molars, better developed infundibula

TABLE 1
Summary of cranial characters

	Z581	<i>quagga</i>	<i>burchelli</i>	<i>zebra</i>
1. Size, smaller or larger	smaller	✓	✓	×
2. Frontals, convex or flat	flat	✓	×	✓
3. Level of fusion of temporal lines, anterior or posterior	posterior	✓	×	✓
4. External auditory meatus, slanted or horizontal	slanted	✓	✓	×
5. Nasal flange behind premaxilla, absent or present	absent	—	✓	×
6. Plane of alisphenoid, slanted or horizontal	slanted	✓	✓	×
7. Styloid process, short or long	short	×	✓	×
8. Occiput, drawn out posteriorly or more upright	more upright	✓	intermediate	×
9. Mastoid, narrow or wide	narrow	✓	✓	×
10. Upper edge of zygomatic arch, curved and rising high or straight and low	curved, high	✓	intermediate	×
11. Anterior part of protocone, elongated or short	elongated	✓	✓	×
12. Cement around cheek teeth, much or less	much	✓	×	✓
13. Deciduous P ¹ , present or absent	present	×	✓	×
14. Infundibula of lower incisors, present or absent	in I ₁ s only	✓	×	×
15. Shape of mandibular symphysis posteriorly, tall or low	tall	✓	✓	×
16. Surface behind lower incisors, flat or concave	flat	✓	×	×

✓ = agreement with Z581; × = difference from Z581; — = character not visible.

in the lower incisors and a flatter mandibular symphyseal surface behind the lower incisors. The poor extent to which the occipital top is drawn out backwardly and the strong curvature of the zygomatic arch are also characters which appear to be more distinctive of *quagga* than of *burchelli*. These findings are in agreement with the photographs of *quagga* skulls in Hilzheimer (1912, pl. 7, fig. 4, pl. 8, pl. 9, figs 3-4). The anterior elongation of the protocone is poorly developed in the Berlin skull A2617 of Hilzheimer, pl. 9, fig. 2, but this skull is not of a quagga (Antonius 1951 : 35).

Three other skull characters have been discussed in the past in relation to *quagga* but have not been used in the comparisons in this paper : diastema length, a pre-orbital cheek depression, and an upwardly bent profile of the anterior part of the nasals. Z581 has a longer diastema than the London *quagga* skull, as seen in the table of measurements, but the latter is unusual among quaggas, Hilzheimer (1912 : 100) giving much greater diastema lengths at 87, 97, 99 and 94 mm, as well as a juvenile at 55 mm. Lydekker (1904 : 428) observed the preorbital depression in the London *quagga* skull and took it as a differentiating character of the species, but similar vestigial depressions appear in some males of other zebras. There is no preorbital depression in Z581. The front part of the nasals is bent slightly upwards in the London *quagga* skull but not in Z581. Such an outline is present in about a third of the *burchelli* sample, although perhaps less frequent in specimens from South West Africa. Hilzheimer (1912 : 93) attributed the strength of this character in the London *quagga* skull to its having come from an animal which had been captive for a long period.

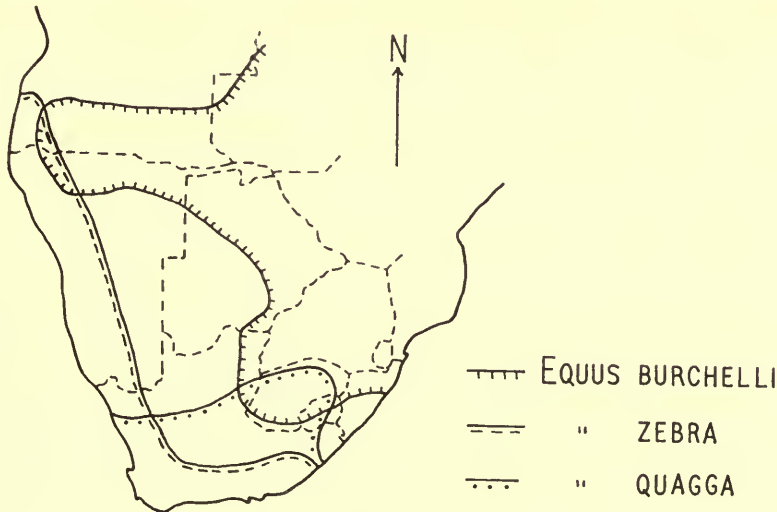


FIG. 2. Map of southern Africa to show the approximate original distributions of three zebra species. The original distributions of *E. quagga* and *E. zebra* are very uncertain, and their overlap may have been less than indicated here. Political boundaries are shown for guidance.

No known skulls of the extinct southernmost race of Burchell's zebra, *E. burchelli burchelli*, were available for use in the comparisons and it might be alleged that their skulls could have resembled *quagga* skulls more closely than do those of other *burchelli* races. As far as skin characters go, it is known that southern populations of *burchelli* tended to lose the posterior striping, and the beginnings of this trend can be seen even in surviving populations of *E. burchelli antiquorum*, the next southernmost race to *burchelli burchelli*. However, this resemblance to *quagga* may be more apparent than real; *quagga* had a brown body colour posteriorly, its posterior striping assumed a pattern unlike *burchelli* as can be seen on mounted skins in Tring and Vienna (Rau, 1974, figs 19, 21), it had no lighter 'shadow' stripes between the more posterior black stripes as seen in southern *burchelli*, and its dark stripes were wider relative to the white ones than in other zebras (also see Cabrera, 1936 : 91-2). It seems likely that both *zebra* and *quagga* were originally zebras of the more arid country lying to the south-west of the range of *burchelli* (Fig. 2), and that there is no need to suppose that skulls of *burchelli burchelli* would have approached those of *quagga* in their morphology.

A SUPPOSED QUAGGA SKULL IN THE CITY MUSEUM, BRISTOL

A male equid skull, Aa 3294, in the City Museum, Bristol, was accessioned in the latter half of 1927 and thought to be of a *quagga*. A pencilled note in the museum register reads: '? S. H. Swayne, 28 June 1872'.

I was able to see this skull on 24 January 1974, and it did not appear to be a *quagga* or any other species of zebra. It showed the following differences from zebras:

- overall size is too small;
- skull width across the orbits exceeds that across the back of the zygomatic arch;
- premaxilla is narrow in side-view (even narrower than in Grevy's zebra), and narrows still more as it rises towards the nasal;
- occiput is rather small;
- braincase roof is too strongly curved in profile.

There are additional differences between the Bristol skull and the *quagga* skull in the British Museum (Natural History):

- the exposed part of the mastoid is too irregular in shape;
- vertical part of the rear median wall of the mandibular symphysis is too low;
- upper edge of zygomatic arch is insufficiently curved in side view;
- too little cement around the side walls and the cheek teeth;
- upper surface of the mandibular symphysis behind the incisors is more concave.

It is not necessary in this paper to provide an alternative identity for Aa 3294. However, its size and morphology agree well with two skulls in the British Museum (Natural History) of a Dartmoor pony and a Shetland pony. The rather small canines agree well with the Shetland pony, Osteology register 1952.4.1.3, and raise the possibility that Aa 3294 comes from a castrated domestic animal. The irregularly shaped mastoid is commoner in horses and ponies than in other equids.

TABLE 2

Measurements taken on the skulls discussed in this paper (mm)

	<i>Equus quagga</i> 1864.7.2.3	Z581	Aa 3294
Skull length, top of occipital crest to front premaxilla	494	482	431
Skull length, anterior edge foramen magnum to front premaxilla	446	442	398
Top of occipital crest to back of orbit	186	181	—
Back of orbit to front premaxilla	349	335	—
Skull width across posterior orbital rims	182	179	183
Skull width across zygomatic arch	174	178	177
Median length of nasals	—	194	171
Nasals breadth above infraorbital foramen	—	50.2	49
Occipital condyle to back M ³ at occlusal surface	209	208	174
Back M ³ at occlusal surface to front premaxilla	274	273	254
Diastema length, I ³ to P ^{I/2} (right side)	73.5	92	65
Occlusal length, M ¹ to M ³	73	69.8	71
Occlusal length, P ^{I/2} to P ⁴	88.2	87.6	89

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PLATE 1

Dorsal view of skull of *Equus quagga*, University College Z581. The scale in this and succeeding plates is marked in centimetres.



PLATE 2

Lateral view of same skull. The old number '41' is written on the mandible just above the number 'Z581'.



PLATE 3

Palatal view of same skull.



PLATE 4

- A. Occipital view of same skull.
- B. Occlusal view of lower dentition of same skull.



A NEW ANGELFISH OF THE GENUS *CENTROPYGE* (TELEOSTEI: POMACANTHIDAE) FROM ASCENSION ISLAND

By ROGER LUBBOCK & RICHARD D. SANKEY

SYNOPSIS

A new species of *Centropyge* is described from Ascension Island ; it is the second pomacanthid to be recorded from Ascension, and the third *Centropyge* to be recorded from the tropical Atlantic ; it appears to be derived from tropical western Atlantic forms.

INTRODUCTION

TO DATE only one species of angelfish (family Pomacanthidae) has been recorded from Ascension Island in the south Atlantic, namely the widespread *Pomacanthus paru* (Bloch), known otherwise only from the tropical western Atlantic (see 'Remarks' below) ; specimens of *P. paru* from Ascension were recorded by Fowler (1919, 1936) and Fraser-Brunner (1933). We examined living juvenile and subadult specimens of *P. paru* from Ascension and various West Indian localities, and on coloration and superficial morphology, they clearly appear to be conspecific. We now report a second species of angelfish from Ascension, belonging to the genus *Centropyge*. Two species of *Centropyge* have previously been recorded from the tropical western Atlantic, *C. argi* Woods & Kanazawa, 1951 and *C. aurantonotus* Burgess, 1974 ; the present species is new to science, and is the third Atlantic species of *Centropyge*. Type specimens are deposited at the British Museum (Natural History) (BMNH) and the United States National Museum (USNM).

Centropyge resplendens n. sp.

Resplendent angelfish
(Fig. 1, Plate 1)

DESCRIPTION. Based on three fishes, 29.0–35.3 mm SL (standard length), from Ascension Island. Measurements are those of the holotype, followed in parentheses by those of the larger and smaller paratypes respectively where these differ from the holotype.

Dorsal fin rays XIV 16 (last ray divided to base) ; anal fin rays III 17 (last ray divided to near base in holotype) ; pelvic fin rays I 5 ; pectoral fin rays 16, first ray rather closely applied to second ray, all rays branched except for upper 2 and lower 2 rays ; 17 principal caudal fin rays, branched with the exception of the uppermost and lowermost rays, which do not quite reach posterior margin ; three small supplementary rays above and below principal caudal fin rays ; pored lateral line scales 34 (35, 34) ; oblique scale rows from upper end of gill opening to caudal base

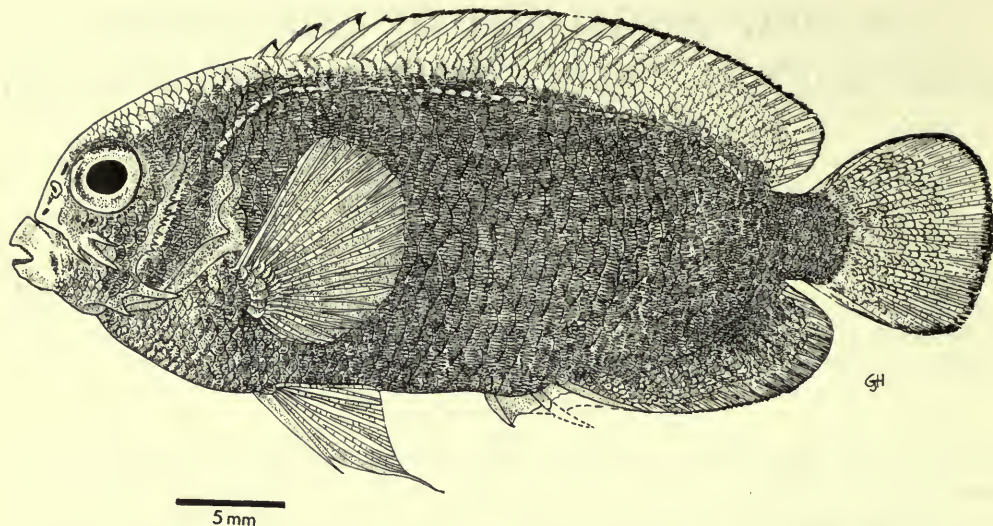


FIG. 1. Holotype of *Centropyge resplendens* n. sp. 35.3 mm SL. Ascension Island.
Drawing by G. Howes.

44 (43, 45); scales above lateral line to origin of dorsal fin 6 (7, 6); scales below lateral line to origin of anal fin 14 (14, 16); circumpeduncular scales 16; gill-rakers on first arch 5 or 6 + 1 + 15 or 16 = 22, the first very small; branchiostegal rays 6; upper teeth in outer series 53 (51, 55); lower teeth in outer series 46 (54, 47).

The following measurements are presented as percentages of the SL. Total length 123.8 (123.8, 122.9); head length (measured from front of upper lip to end of opercular membrane) 30.0 (30.7, 31.3); snout length 9.9 (9.0, 10.4); orbit diameter 11.9 (12.1, 13.3); bony interorbital width 7.1 (7.6, 6.4); predorsal length 36.3 (37.2, 40.2); depth at first dorsal spine 43.1 (44.1, 47.4); body width behind gill opening 18.7 (16.9, 16.5); least depth of caudal peduncle 11.6 (11.4, 12.0); length of caudal peduncle (measured horizontally from rear base of dorsal fin to caudal base) 7.6 (8.6, 7.2); length of longest pectoral fin ray 22.1 (24.1, 24.1); length of longest pelvic fin ray 26.1 (28.6, 28.9); dorsal fin base length 65.7 (65.5, 64.3); lengths of first, second, third and fourth dorsal spines 4.5 (6.6, 5.6), 8.8 (11.4, 11.2), 11.9 (12.4, 16.9) and 11.3 (12.4, 14.5) respectively; anal fin base length 35.4 (35.9, 36.1); lengths of first, second and third anal spines – (9.7, 11.2), – (12.1, 14.1), and – (13.4, 14.5) respectively (anal spines clearly deformed in holotype, not measured).

Body deep and relatively compressed. Mouth small, terminal, the gape horizontal; maxilla reaching slightly posterior to vertical from anterior nostril; upper lip approximately as broad (vertically at front) as lower, upper lip height about a third of orbit diameter.

Teeth slender and elongate, close-set, flexible, tricuspid (the central cusp notably longer and broader than the lateral ones), in two principal rows in jaws, the teeth of the outer row largest; no teeth on roof of mouth; tongue short and broadly rounded.

Gill membranes narrowly attached to isthmus; 5 (5, 7) fleshy papillae in mid-ventral line between chin and isthmus; anterior and posterior nostrils separated by a space about a third to a half of length of posterior nostril; posterior nostril oval, slightly larger than round anterior nostril, separated from eye by a space about equal to its width; anterior nostril with a short membraneous tube with an elevated posterior flap.

A stout spine at corner of preoperculum, its length about three-quarters of orbit diameter; 20 (25, 23) small spines of somewhat irregular size along upper margin of preoperculum and one spine on lower edge of preoperculum, about a third (about a fifth in paratypes) as long as spine at angle; 2 smallish spines on interoperculum; a few small spines on suboperculum; operculum with 2 broad flat spines, one near upper end of gill opening and the other at about the level of the lower edge of eye; preorbital with 3 (2, 2) spines along ventral edge.

Scales coarsely ctenoid (up to about 20 ctenii on margins), the exposed portion ridged; from fourth dorsal spine onwards, dorsal fin with scaly base, scalation extending over three-quarters if not virtually all of fin on median and posterior portion; anal fin with scaly base, scalation extending over three-quarters or more of fin on median and posterior portion; scales on basal half of caudal fin, with small scales extending out on fin rays for about a third more of length of fin; pectoral fins scaled only basally; pelvic fins with small scales extending out on fin rays for up to three-quarters of length of spine. Head almost completely scaled.

Lateral line steeply arched anteriorly, ending below posterior part of dorsal fin.

Origin of dorsal fin slightly posterior to vertical through upper angle of gill opening; membranes of anterior portion of dorsal fin, between first and second, second and third, and third and fourth spines, deeply incised, while those between posterior spines and rays only slightly if at all indented. Membranes of anterior portion of anal fin, between first and second, and second and third spines deeply incised, while those between posterior rays not indented. Caudal fin nearly truncate. Pectoral fins more or less rounded, not reaching to level of origin of anal fin. Origin of pelvic fins below base of pectoral fins; first pelvic soft ray prolonged, reaching spinous part of anal fin base, about a third as long again as pelvic spine.

Coloration: In life, head and body bright to dark blue; snout bright yellow-orange; chest with orange tinges; bright yellow-orange to orange stripe from snout between eyes along dorsal body contour onto upper part of caudal peduncle. Orbit ringed with bright blue; iris orange. Dorsal fin bright yellow-orange to orange with dark blue distal margin; anal fin bright to dark blue, becoming bluish orange distally and posteriorly, with bright blue distal margin; pelvic fins dusky bluish orange with bright blue anterior margin; pectoral fins hyaline; caudal fin bright yellow-orange to orange with dark blue distal margin.

In alcohol, bright to dark blue markings become brown to dark brown; yellow-orange to orange markings become beige on body, beige to hyaline on fins.

REMARKS. As was pointed out by Randall & Caldwell (1973), 'All of the species of *Centropyge* are very similar in body form and counts, but they are distinctive in colour pattern'. The colour pattern of *Centropyge resplendens* (see above and Plate 1)

is quite distinctive and separates it clearly from all known species. As might be expected, *Centropyge resplendens* is closest to *C. argi* Woods & Kanazawa and to *C. aurantonotus* Burgess, both restricted to the tropical western Atlantic. *Centropyge argi* has a dark blue body, but only the head and chest are yellow to orange (see colour illustrations in Burgess, 1974, and Böhlke & Chaplin, 1968). *Centropyge aurantonotus* also has a dark blue body but with orange head, chest, dorsal body contour and dorsal fin (see colour illustration in Burgess, 1974). *Centropyge aurantonotus* differs from *C. resplendens* in the coloration of the caudal fin and of the dorsal margin of the caudal peduncle, which are dark blue in *C. aurantonotus* but yellow-orange to orange in *C. resplendens*; also, the head of *C. aurantonotus* is orange, while that of *C. resplendens* is bright to dark blue, with only the snout and dorsal contour yellow-orange to orange.

Briggs (1974) stated that much of Ascension Island's shore fauna was apparently derived from the western Atlantic, and that some justification existed for placing Ascension in the West Indian Province of the Western Atlantic Region. Only two Pomacanthidae are known from Ascension: *Centropyge resplendens*, which is closely related to tropical western Atlantic forms (no *Centropyge* is known as yet from the eastern Atlantic), and *Pomacanthus paru*, which is otherwise recorded only from the tropical western Atlantic. (The only record of *P. paru* from the eastern Atlantic is that of Fowler, 1936, who considered that *Chaetodon leachii* Bowdich from Madeira was probably *P. paru*; having read the original description of *C. leachii*, we find it most unlikely that *C. leachii* is synonymous with *P. paru*.) The derivation of Ascension Pomacanthidae appears *prima facie* to be in accordance with Briggs' statement, although it should be emphasized that the pomacanthid fauna of the eastern Atlantic is still relatively poorly known, making genuine comparison difficult.

ETYMOLOGY. The name *resplendens* is derived from the Latin for resplendent, and refers to the beautiful coloration of this species.

MATERIAL EXAMINED. (a) *Holotype*, 35.3 mm SL, among coral boulders at 20 m, Ascension Island, coll. G. Earnshaw in December 1974; BMNH 1974.12.20.1. (b) *Paratype*, 29.0 mm SL, coll. with (a); BMNH 1974.12.20.2. (c) *Paratype*, 24.9 mm SL, coll. with (a); USNM.

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R. D. SANKEY
24 HILL CLOSE
STANMORE
MIDDLESEX

PLATE I

Holotype of *Centropyge resplendens* n. sp. 35.3 mm SL. Ascension Island.
Aquarium photograph by R. Lubbock.



A NEW SPECIES OF *NANOCHROMIS* (PISCES, CICHLIDAE) FROM THE OGOWE SYSTEM, GABON

By ETHELWYNN TREWAVAS

AMONG the fishes collected by the Cambridge Expedition of 1957 to Gabon is a single specimen of a cichlid of an undescribed species. Unwilling to describe it from a single specimen, I had put it aside, but recent renewed interest in the ichthyology of Gabon persuades me to call attention to it and name it. Recently Thys van den Audenaerde & Loïselle (1971) have described two species of *Nanochromis* from Ghana and Ivory Coast, one of which is so similar to the Gabonese fish as to require close comparison with it.

Nanochromis gabonicus sp. nov.

HOLOTYPE: ♀, 47 + 13 mm, from a pool by the road from Mitzic to Medouneu, probably in the drainage basin of R. Okano, tributary of the Ogowe. BMNH 1967.10.12.57.

CHARACTERS OF GENERIC IMPORTANCE. Pad on roof of pharynx with a groove around its antero-lateral edge and covered with tubercles resembling, under low magnification, the batteries of taste-buds of the pad of *Chromidotilapia* (see Trewavas, 1974, pl. 4). Microbranchiospines absent. Outer ceratobranchial gill-rakers with two subequal tubercles. At least in female, first and second soft pelvic rays approximately equal, not produced, but coming to a blunt point. Last scale of upper lateral line separated from dorsal fin by only a half-scale. Scales cycloid, the circuli parallel to the edge of the scale (roman), except a few with a gothic arrangement.

Although the base of the skull was not examined in this unique specimen, the other characters indicate that it belongs to the group in which the apophysis for the pharyngeals is formed by the parasphenoid alone.

DISTINGUISHING SPECIFIC CHARACTERS. A black spot at the tip of each pelvic fin (♀). Chest completely covered with imbricating scales.

DESCRIPTION. Proportions as % SL: length of head 35, of pectoral fin 20.5, length and depth of caudal peduncle 13.8.

Proportions as % length of head: snout 39.4, diameter of eye 27, depth of pre-orbital 21, interorbital width 21, length of lower jaw 36.5.

Two series of small scales on the left cheek, two and a short third series on right; a naked patch below them.

Teeth all unicuspid, in two series in upper jaw, 2-3 in lower; 52 in outer series of upper jaw.

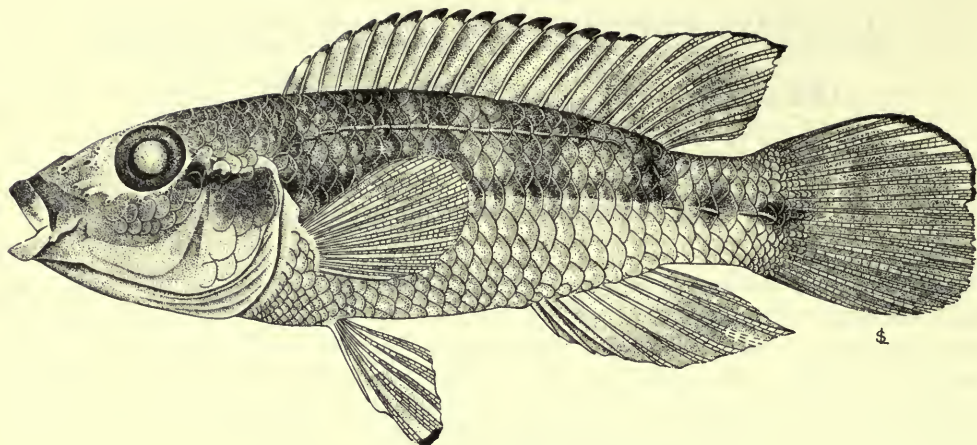


FIG. 1. *Nanochromis gabonicus*, holotype.

Lower pharyngeal bone deeply indented posteriorly, with short blade and rather few, pointed, bicuspid teeth.

Gill-rakers $5 + 1 + 8$ on first arch.

Scales 28 in the lateral line series, the upper lateral line piercing 19 scales, the lower 4 on the left side, 8 on the right, the last of which is on the caudal fin; 3 between origin of dorsal and lateral line; 3 between bases of pectoral and pelvic fins; immediately in front of this row the scales are smaller, but the chest is completely covered with imbricating scales; 12 around the caudal peduncle.

Vertebrae 27 (12 + 15).

Dorsal XV 9; last spine 12% SL. Anal III 7; third spine 13.8% SL.

Pectoral fin rounded. Pelvic with first two soft rays approximately equal, not produced, just reaching vent when laid back. Caudal rounded at the corners, the straight edge in the middle involving $3\frac{1}{2}$ upper and $3\frac{1}{2}$ lower rays.

Colour in general pale, top of head darker. A dark bar from eye to top of operculum and a dark band along middle of side to base of caudal, emphasized in five or six places; traces of three broad blotches from dorsum, tapering towards lateral band. Dorsal lappets and upper edge of soft dorsal black. Postero-dorsal edge of caudal black with a white submarginal band; a black spot at the tip of each pelvic fin.

The ovaries of this small fish are partly discharged, still containing a few eggs of about 1.3 mm diameter as well as some smaller oocytes.

This specimen (and probably the species to which it belongs) differs from *N. cavalliensis* Thys & Loisel in the blunt pelvic fin and the absence of any prolongations of caudal rays, but it is smaller than the holotype (also a ♀) of that species. It also has a wider interorbital region, more teeth in the upper jaw (cf. 42 in *N. cavalliensis*) and a slightly shorter pectoral fin. No black marginal and white submarginal bands were described on the caudal of *N. cavalliensis* and in that species ripe eggs were 2.0×1.5 mm. Those in the type of *N. gabonicus* may of course be unripe, of a batch to follow those recently shed.

DISCUSSION. The type species of *Nanochromis* Pellegrin, *N. nudiceps* (Boulenger), inhabits swiftly running water and has characters associated with this habit, namely scaleless chest, middle soft rays of pelvic fin longer than the others. In it scales are also absent from the cheek, top of head and a narrow strip along the back on each side of the base of the dorsal fin ; both lateral lines are interrupted.

Matthes (1964 : 134) has re-examined the types of the other two nominal species, *N. dimidiatus* Pellegrin, 1900 (from Banghi) and *N. squamiceps* (Boulenger) from R. Lindi, Congo system, and finds that both fall within the range of variation of specimens from Lake Tumba basin regarded by him as a single species. In the British Museum four specimens of *N. dimidiatus* collected at Banghi on two separate occasions show that the incomplete squamation is maintained, at least in that population. Thys, in an addendum to his paper of 1968, claims to have evidence from living specimens that they are distinct.

Thys also refers to an unnamed (new) species from R. Ivindo, tributary of the Ogowe, which he relates to *N. squamiceps*. From his brief characterization of this I believe it must be a species of which Dr Géry has sent me a few specimens. I mention it here to state that it differs from *N. gabonicus* in having the pelvic fin a little more acute in the female (much more in the male), with a black streak along the first soft rays but no black spot at its tip, a broad naked area on the chest on either side of a median row of scales and very small scales on the nape and occiput. As in *N. gabonicus*, the vertical fins of the female are clear or lightly peppered except at the edges ; in the male they bear conspicuous series of spots.

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THE FIRST ZOEAL STAGES OF *CANCER* *PAGURUS* L., *PINNOTHERES PISUM* (PENNANT) AND *MACROPHTHALMUS DEPRESSUS* RÜPPELL (CRUSTACEA, DECAPODA, BRACHYURA).

By A. L. RICE

SYNOPSIS

The first zoeal stages in *Cancer pagurus*, *Pinnotheres pisum* and *Macrophthalmus depressus* are described and larval characters within their respective families are discussed.

INTRODUCTION

ALTHOUGH there are published accounts of one or more larval stages of several hundreds of brachyuran species, less than one hundred of these descriptions include a significant amount of detail. Consequently, while there has been a welcome tendency in recent years for larval papers to deal with all the developmental stages of crabs reared in the laboratory, there is still a need for detailed re-descriptions, even of single zoeal stages, where the previous accounts are clearly inadequate. The purpose of this paper is to provide such details of the first zoeal stages of three crabs from material in the larval collections of the British Museum (Natural History).

Cancer pagurus

Larvae hatched from a female collected at Lulworth Cove, Dorset, June, 1973.
B.M.(N.H.) registration no. 1975 : 66.

Dimensions : Tip of dorsal to tip of rostral spines : 2.4–2.6 mm.

Tip to tip of lateral carapace spines : 1.0–1.1 mm.

Carapace (Fig. 1a, b) :

Dorsal carapace spine straight or with a very slight backward curve, about twice as long as the carapace and slightly longer than the straight rostral spine. Rostral spine with minute spinules. Lateral spines about half carapace length. Carapace with a low anterio-median papilla, a pair of setae at the base of the dorsal spine and postero-lateral margins without sub-marginal setae.

Antennule : Simple, with 2 or 3 aesthetascs and a single seta.

Antenna (Fig. 1c) : Spinous process slightly more than half length of rostrum, with spinules on the distal two-thirds increasing in size towards the tip. Exopod about one-third length of spinous process, with 1 long terminal seta and 2 shorter ones, of which 1 is fused.



FIG. 1. *Cancer pagurus*, first zoea: a, lateral view; b, frontal view; c, antenna; d, maxillule; e, maxilla; f, first maxilliped (exopod omitted); g, endopod of second maxilliped; h, telson; j, detail of telson; k, detail of telson in the third zoea of *C. anthonyi*. Bar scale represents 0.5 mm for a, b and h, and 0.25 mm for c-g, j and k.

Maxillule (Fig. 1d): Endopod of 2 segments, with 1 and 6 setae respectively.

Maxilla (Fig. 1e): Endopod bilobed with 3+5 (occasionally 4) setae; scaphognathite with 4 marginal setae and a long plumose posterior projection.

First maxilliped (Fig. 1f) : Basis with 10 setae (arranged 2, 2, 3, 3) ; endopod segments with 3, 2, 1, 2 and 4 + 1 setae ; exopod with 4 natatory setae.

Second maxilliped (Fig. 1g) : Basis with 4 setae ; endopod of 3 segments with 1, 1 and 6 setae.

Abdomen (Fig. 1a) : Somite 2 with forwardly directed dorso-lateral knobs ; somites 2–5 each with a pair of dorso-posterior setae and slight projections on the posterior-lateral margins.

Telson (Fig. 1h, j) : Forks long, slender and divergent, each with one lateral and one dorsal spine, and minute spinules distally ; inner posterior margin with a deep, rounded median notch and three pairs of processes armed with short setules and spinules, those of the distal one-third of the outer process being particularly stout and tooth-like.

DISCUSSION.

The larvae of *Cancer pagurus* were first hatched by Thompson in 1829 and have subsequently been described many times (see Lebour, 1928a). However, with the exception of Williamson's (1910) account, most of these descriptions are very inadequate and the larvae of several Pacific species of the genus are much better known than are those of *C. pagurus*. Thus, Aikawa (1937) published details, including appendage setation, of the first stage of *C. gibbosulus* (de Haan), Mir (1961) compared the first zoeae of *C. magister* Dana, *C. antennarius* Stimpson and *C. anthonyi* Rathbun, Poole (1966) described the complete development of *C. magister*, and Trask (1970, 1974) has similarly dealt with *C. productus* Randall and *C. anthonyi*. From these accounts, including the details of *C. pagurus* given here, it is now possible to define generic, and possibly familial, zoeal characters.

All of the *Cancer* zoeae so far known possess well-developed dorsal, rostral and lateral carapace spines, antennae with spinous processes more than half as long as the rostrum, the two-segmented endopod of the maxillule with 1 + 4 to 1 + 6 setae, the endopod of the maxilla with at least six setae, usually arranged in two distinct groups, lateral knobs on only the second abdominal somite and the telson furcae with one lateral and one dorsal spine. In all the species, with the exception of *C. anthonyi*, the proximal segment of the endopod of the first maxilliped is described as carrying three setae and this, together with the characters listed above, distinguishes these *Cancer* zoeae from those of all other known brachyurans. Mir also recorded three setae on this segment in his first-stage *C. anthonyi* but Trask (1974) reported only two setae in all five stages of his reared material. This character seems generally to be rather conservative amongst brachyuran zoeae, at least within genera* and often within whole families, so that it seemed at least possible that Trask was mistaken. However, I have been able to examine Trask's material and can confirm that *C. anthonyi* does differ from the other known species in this respect. But this species possesses the strong tooth-like spines on the outer posterior telson process (see Fig. 1j, k) which seem to be typical of *Cancer* zoeae and which have

* For instance, a re-examination of the material of *Corystes cassivelaunus* described by Ingle & Rice (1971) revealed that the first zoea carries three setae on this segment, as in the later stages, and not two as figured in that paper.

otherwise been reported only in the closely related *Atelecyclus rotundatus* (Olivi) (Bourdillon-Casanova, 1960).

***Pinnotheres pisum* (Pennant)**

Larvae hatched in July, 1971, from a female collected at Plymouth, Devon.

B.M.(N.H.) registration no. 1975 : 67.

Dimensions : Tip of rostral spine to mid-dorsal point of the carapace : 0.60 mm.

Tip to tip of lateral carapace spines : 0.55 mm.

Carapace (Fig. 2a, b) :

Rostral spine about half carapace length, with a slight forward curve. Lateral spines arise close to the postero-lateral carapace margins, directed downwards and slightly backwards. No dorsal spine, but with a pair of setae close to the mid-dorsal line of the carapace.

Antennule (Fig. 2d) : Reduced to small hemispherical buds carrying 2 aesthetascs and a single seta.

Antenna : Totally absent.

Maxillule (Fig. 2e) : Endopod of two segments carrying 0 and 5 setae respectively.

Maxilla (Fig. 2f) : Coxal and basal endites not clearly bilobed ; endopod with 3 setae, of which 2 are more or less terminal ; scaphognathites with 3 marginal setae and a long plumose posterior process.

First maxilliped (Fig. 2g) : Basis with 2, 2, 3, 3 setae ; endopod segments with 2, 2, 1, 2 and 4 + 1 respectively ; exopod with 4 natatory setae.

Second maxilliped (Fig. 2h) : Basis with 4 setae ; endopod of 2 segments with 0 and 4 or 5 setae ; exopod with 4 natatory setae.

Abdomen (Fig. 2c) : Somites 2 and 3 with small dorso-lateral knobs, those of the second somite joined by a slight ridge over the dorsal surface. Somites 4 and 5 widening to the tri-lobed telson ; rounded median lobe not protruding beyond the acute lateral lobes ; three setose processes between the median and lateral lobes on each side.

DISCUSSION.

Lebour (1928a, b) described the first stage of *P. pisum* hatched from the egg and attributed to the same species a second-stage zoea taken in the plankton. Her description is very inadequate, but where comparison is possible it agrees with that given here except that Lebour was able to detect the rudimentary antenna and found the median telson lobe to overreach the lateral lobes.

The available descriptions of the larvae of other species of *Pinnotheres* indicate that there is a good deal of morphological variation within the genus. Thus, while the zoeae of *P. pinnotheres* (L.) (= *veterum*) and *P. maculatus* Say possess dorsal, rostral and lateral carapace spines (see Hyman, 1925 ; Labour, 1928a, b ; Costlow & Bookhout, 1966), the dorsal spine is absent in *P. pisum* and *P. placunae* (Hornell and Southwell) (Lebour, 1928a, b ; Hashmi, 1970 ; this paper), the laterals are absent in *P. taylori* Rathbun (Hart, 1935), while none of the carapace spines are present in *P. ostreum* (Say) (Hyman, 1925 ; Sandoz & Hopkins, 1947). Similarly,

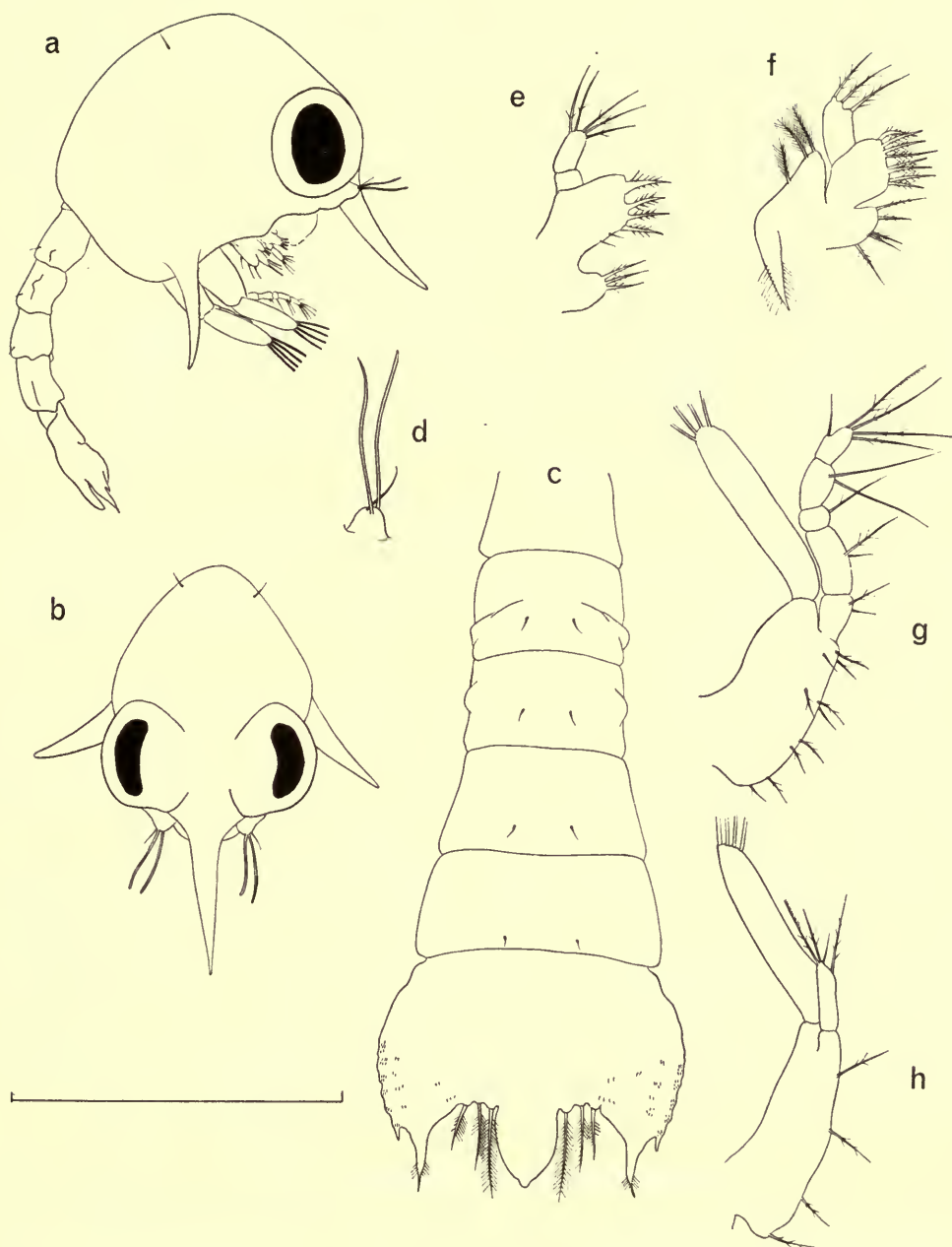


FIG. 2. *Pinnotheres pisum*, first zoea: a, lateral view; b, frontal view; c, abdomen; d, antennule; e, maxillule; f, maxilla; g, first maxilliped; h, second maxilliped. Bar scale represents 0.5 mm for a and b, and 0.25 mm for c-h.

while *P. pisum*, *P. pinnotheres*, *P. placunae* and *P. ostreum* possess the very characteristic trilobed telson which has been found only in the Pinnotheridae, in *P. maculatus* and *P. taylori* the telson is the much more typical brachyuran forked type. The degree of development of the antennules and antennae is also very variable, these appendages being greatly reduced or even absent, at least in the early stages, in *P. ostreum*, *P. placunae* and *P. pisum*, moderately developed in *P. taylori*, and quite normal in *P. maculatus*. The number of zoeal stages also varies within the genus, with *P. pinnotheres* and *P. taylori* having only two zoeae, *P. placunae* probably having three, *P. ostreum* four and *P. maculatus* five. One result of this variation in development rate is that the pleopods make their appearance at different stages in the different species, these appendages appearing as buds in the third stage in *P. ostreum* and the fourth in *P. maculatus*, but being well developed by the third stage in *P. placunae* or even as early as the second stage in *P. pinnotheres* and *P. taylori*. Finally, as Costlow & Bookhout (1966) point out, *P. maculatus* seems to have a far more typically 'brachyuran' development than any of the other described species, since it is apparently the only one in which the sixth abdominal somite is separated from the telson in the late zoeal stages.

Clearly, then, there is no difficulty in distinguishing between the known zoeae larvae of *Pinnotheres* species. A more difficult problem may be the recognition of characters common to the zoeae of *Pinnotheres* or of the Pinnotheridae generally, which will distinguish them from other crab larvae even where, as in *P. taylori*, neither the characteristic trilobed telson nor the postero-ventrally directed lateral carapace spines are present.

Firstly, in all those species for which the information is available the endopod of the maxilla carries only three setae and these are arranged in a single more or less terminal group, or at least not clearly divided into two distinct groups. This character at once distinguishes the Pinnotheridae from almost all other brachyuran larvae, for such a setal armature has been recorded outside this family only in the Leucosiidae and the ocypodid sub-family Ocypodinae (see also below).

The three-segmented endopod of the second maxilliped readily distinguishes these ocypodids from both the Leucosiids and the pinnotherids in which this endopod never has more than two joints. Finally, while there are a number of differences between the pinnotherids and the leucosiids in the detailed morphology of the appendages, the most obvious distinction is the simple triangular telson with the closely spaced row of six processes on the relatively straight posterior margin which has been found in every leucosiid zoea so far described; this contrasts strongly with both the tri-lobed telson and the more typical fork found in the Pinnotheridae.

Macrophthalmus depressus Rüpell

Larvae hatched in Bahrain, Arabian Gulf, from a female collected from the foreshore at Jufair in March, 1974.

B.M.(N.H.) registration no. 1975 : 68.

Dimensions : Tip of dorsal to tip of rostral spines : 0.66 m.m.

Maximum width across carapace : 0.29 mm.

Carapace (Fig. 3a, b) :

Slender dorsal and rostral spines, each about half the carapace length ; lateral spines absent. A pair of short setae at the base of the dorsal spine. Postero-ventral edge of carapace with a small tooth and a slightly crenulate margin, but without sub-marginal setae.

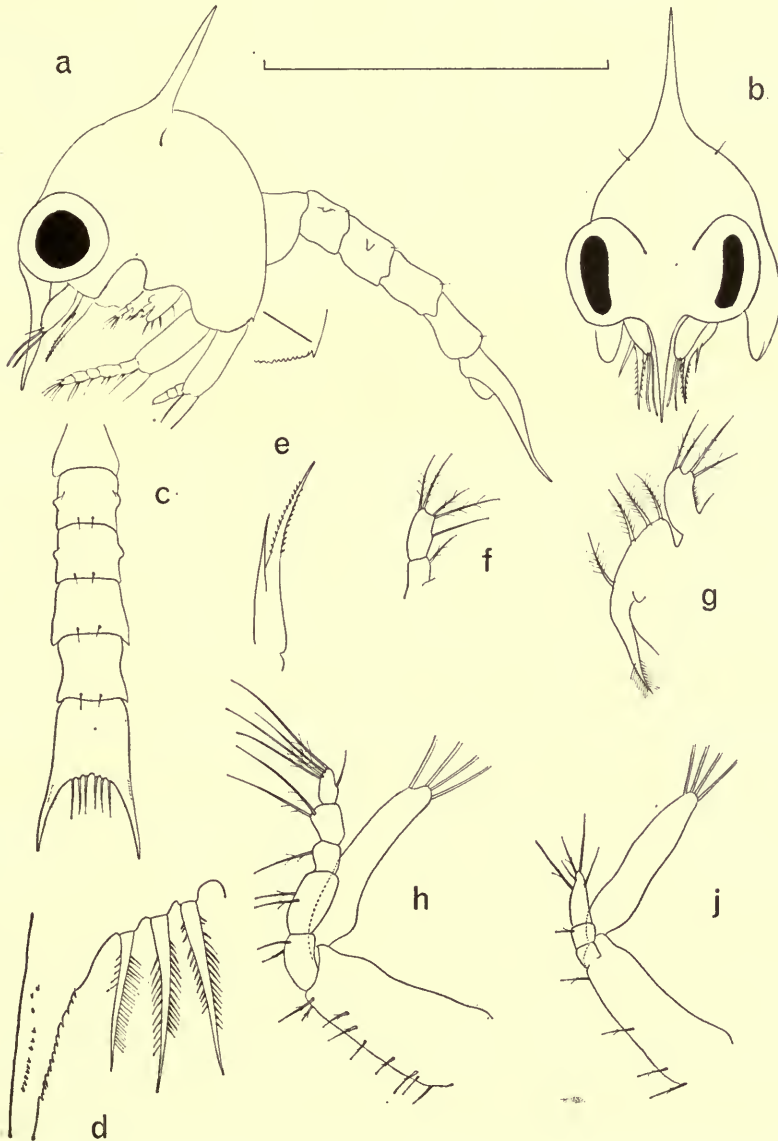


FIG. 3. *Macrophthalmus depressus*, first zoea : a, lateral view ; b, frontal view ; c, abdomen ; d, detail of telson ; e, antenna ; f, endopod of maxillule ; g, maxilla ; h, first maxilliped ; j, second maxilliped. Bar scale represents 0.5 mm for a-c, 0.25 mm for e-j, and 0.1 mm for d.

Antennule (Fig. 3b) : Simple, with 2 terminal aesthetascs and 1 seta.

Antenna (Fig. 3e) : Spinous process slightly shorter than rostrum ; exopod a simple, unarmed spine slightly more than half the spinous process.

Maxillule (Fig. 3f) : Endopod of 2 segments with 1 and 5 setae respectively.

Maxilla (Fig. 3g) : Endopod with 2 + 2 setae ; scaphognathite with 4 marginal setae and a long, plumose posterior process.

First maxilliped (Fig. 3h) : Basis with 9 or 10 setae ; endopod segments with 2, 2, 1, 2 and 4 + 1 setae ; exopod with 4 natatory setae.

Second maxilliped (Fig. 3j) : Basis with 4 setae ; endopod of 3 segments with 0, 1 and 5 setae respectively ; exopod with 4 natatory setae.

Abdomen (Fig. 3c) : Somites 2 and 3 with dorso-lateral knobs ; somites 2-5 each with short postero-lateral processes and a pair of short setae close to the dorso-posterior margin. Telson widening only slightly posteriorly, the forks about the same length as the body of the telson. Posterior margin with three pairs of process which are naked distally (see Fig. 3d). Telson forks unarmed except for two rows of minute spinules basally.

DISCUSSION.

Hashmi (1969) described the first zoeae of five species of *Macrophthalmus*, including *M. depressus*. In general, Hashmi's account agrees very closely with that given here, except in the details of the setation of the maxillipeds. For instance, Hashmi gives the setal formula of the endopod of the first maxilliped as 1, 2, 1, 2, 5, whereas with the exception of his own account of *M. crinitus* Rathbun and the larvae of *Dotilla blanfordi* Alcock and *D. sulcata* (Forskål) (Rajabai, 1959 ; Ramadan, 1940) the proximal segment carries two setae in every ocypodid larva for which this information is known, and the typical setal formula for the family seems to be 2, 2, 1, 2, 5.

Similarly, Hashmi records a seta on the basal segment of the endopod of the second maxilliped whereas I was unable to find a seta in this position in my material and it seems to be unusual in the family as a whole (Table 1).

Using characters of the carapace spines, antennae, telson, maxillae and maxillipeds Aikawa (1937) was able to separate zoeae of the ocypodid genera *Macrophthalmus*, *Tympanomerus* (= *Ilyoplax*), *Scopimera* and *Uca* into groups corresponding to the three sub-families based an adult taxonomy. Thirty years later Wear (1968) re-examined the larval situation within the Ocypodidae, information on the larvae of fourteen species belonging to seven genera by then being available, but was unable to obtain any support for the adult classification. However, in separating the larvae into groups Wear gave greatest significance to the presence or absence of lateral carapace spines, and somewhat lesser significance to the form of the abdomen and the degree of development of the antennal exopod. There is, however, a good deal of evidence to suggest that the setation of the mouthparts may reflect taxonomic divisions between larvae more effectively than these more 'obvious' characters. Certainly, on the basis of the setation of the endopods of the maxillules, maxillae and of the second maxillipeds the described ocypodid larvae fall into distinct groups, which correspond rather well with the accepted sub-families (Table 1).

TABLE I

Setation of the maxillae and the second maxilliped, the number of telson fork spines, and the presence or absence of lateral carapace spines in described ocypodid zoeae

	Maxillule endopod	Maxilla endopod	Maxilliped 2 endopod	Telson fork spines	Lateral carapace spines	Source
MACROPHTHALMINAE						
<i>Macrophthalmus depressus</i>	1, 5	2, 2 (4)	0, 1, 5	0	—	This paper
<i>Macrophthalmus depressus</i>	1, 5	2, 2 (4)	1, 1, 5	0	—	Hashmi, 1969
<i>Macrophthalmus depressus</i>	1, 6	2, 2 (4)	1, 1, 6	0	—	Aikawa, 1929
<i>Macrophthalmus dilatatus</i>	1, 5	2, 2 (4)	1, 1, 6	0	—	Aikawa, 1929
<i>Macrophthalmus japonicus</i>	1, 5	2, 2 (4)	1, 1, 6	0	—	Aikawa, 1929
<i>Macrophthalmus sulcatus</i>	1, 5	2, 2 (4)	1, 1, 6	0	—	Hashmi, 1969
<i>Macrophthalmus latreillis</i>	1, 5	2, 2 (4)	0, 1, 6	0	—	Hashmi, 1969
<i>Macrophthalmus pacificus</i>	1, 5	2, 2 (4)	0, 1, 5	0	—	Hashmi, 1969
<i>Macrophthalmus crinitus</i>	1, 4	2, 3 (5)	0, 1, 6	2	+	Hashmi, 1969
<i>Hemiplax hirtipes</i>	1, 5	2, 2 (4)	0, 1, 6	0	+	Wear, 1968
OCYPODINAE						
<i>Ocypode quadrata</i>	0, 5	1, 2 (3)	0, 0, 5	0	+	Diaz & Costlow, 1972
<i>Ocypode platytarsis</i>	—	1, 2 (3)	0, 0, 4	0	+	Rajabai, 1951
<i>Ocypode gaudichaudii</i>	0, 4	1, 2 (3)	0, 0, 5	0	+	Crane, 1940
<i>Uca annulipes</i>	0, 4	1, 2 (3)	0, 0, 4	0	—	Feest, 1969
<i>Uca annulipes</i>	0, 4	1, 2 (3)	0, 0, 4	1	—	Hashmi, 1968
<i>Uca marionis</i>	0, 4	1, 2 (3)	0, 0, 5	0	—	Hashmi, 1968
<i>Uca pugilator</i>	0, 4	1, 2 (3)	0, 0, 4	0	—	Hyman, 1920
<i>Uca pugnax</i>	0, 4	1, 2 (3)	0, 0, 4	0	—	Hyman, 1920
<i>Uca minax</i>	0, 4	1, 2 (3)	0, 0, 4	0	—	Hyman, 1920
<i>Uca triangularis</i>	0, 4	1, 2 (3)	0, 0, 4	0	—	Feest, 1969
SCOPIMERINAE						
<i>Scopimera globosus</i>	0, 5	2, 3 (5)	0, 1, 6	0	+	Aikawa, 1929
<i>Dotilla sulcata</i>	0, 4	2, 3 (5)	—	0	+	Gohar & Al- Kholy, 1957
<i>Dotilla sulcata</i>	0, 4	2, 2 (4)	0, 2, 4	0	+	Ramadan, 1940
<i>Dotilla blanfordi</i>	0, 4	2, 3 (5)	1, 1, 4	0	—	Rajabai, 1959
<i>Ilyoplax pusillus</i>	0, 4	2, 3 (5)	1, 1, 5	0	+	Aikawa, 1929
<i>Ilyoplax gangetica</i>	0, 4	(4-5)	0, 5	0	—	Feest, 1969
MICTYRIDAE ?						
<i>Mictyris longicarpus</i>	1, 5	2, 2 (4)	1, 1, 6	0	—	Cameron, 1965

Thus the zoeae of the genera *Macrophthalmus* and *Hemiplax* (sub-family Macrophthalminae) all have the basal segment of the endopod of the maxillule armed with a single seta, the endopod of the maxilla armed with a total of four or five setae, and the middle segment of the endopod of the second maxilliped carrying a single seta. In contrast, the genera *Ocypoda* and *Uca* (sub-family Ocypodinae) have both the basal segment of the endopod of the maxillule and the middle segment of the endopod of the second maxilliped unarmed, while the endopod of the maxilla carries a total of only three setae. Larvae of the third sub-family, the Scopimerinae, represented

by the genera *Scopimera*, *Ilyoplax* and *Dotilla*, show a combination of these characters which tend to exclude them from both of the other two groups. Finally, the first zoea of *Mictyris longicarpus* Latreille has setal characters similar to those of the Macrophthalminae but, as pointed out by Wear (1968), it possesses other characters, including the absence of both dorsal and lateral carapace spines and the form of the telson, which may support Balss' (1957) separation of *Mictyris* into a distinct family.

Table 1 also includes data on the armature of the telson forks and the presence or absence of lateral carapace spines, showing that these characters are not correlated with the sub-family groups but vary even within the same genus.

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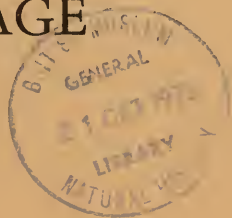
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THE HYDROID SPECIES OF *OBELIA*
(COELENTERATA, HYDROZOA:
CAMPANULARIIDAE), WITH NOTES
ON THE MEDUSA STAGE



P. F. S. CORNELIUS

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BY
PAUL FREDERICK SINEL CORNELIUS

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SYNOPSIS

The genus *Obelia* Péron & Lesueur, 1810a, is redefined and nominal taxa already described from the hydroid stage are assessed. Three species are considered valid, *O. bidentata* Clarke, 1875, *O. dichotoma* (Linnaeus, 1758) and *O. geniculata* (Linnaeus, 1758). Each is diagnosed, redescribed and illustrated with notes on morphological variation, nematocysts, identification, nomenclature, synonymy, type specimens and distribution. Owing to the paucity of information the many species described from the medusa stage cannot yet be evaluated or related to the hydroids. The affinities of those species of hydroids no longer assigned to *Obelia* are discussed briefly. The genus *Laomedea* Lamouroux, 1812, is reduced to a synonym of *Obelia* but the genus *Campanularia* Lamarck, 1816, is regarded as valid.

INTRODUCTION

In many genera of hydromedusae there is specific diversity of the medusa generation while the hydroid stage appears uniform. However, in the genus *Obelia* Péron & Lesueur, 1810a, the reverse is the case and it is the medusae which cannot be distinguished. Thus, as summarized by Russell (1953), medusae liberated from the hydroid species *Obelia dichotoma* (Linnaeus, 1758) and *O. geniculata* (Linnaeus, 1758) and reared to maturity appear morphologically identical, both being referable to the medusa *O. lucifera* (Forbes, 1848) as known from the plankton. Further

confusion results from the large number of species that has been described from the hydroid, some seventy having been proposed between 1830 and 1948. It seemed timely to evaluate the systematic criteria on which these species were proposed, hopefully to provide a basis for evaluating taxa described from the medusa. Previously, the genus had been fully revised only in the publications of Bedot (1901, 1905, 1910, 1912, 1916, 1918, 1925) who recognized thirty-seven hydroid species described up to the end of 1910. In the present work, however, these and subsequently described species are referred to only three nominal species. Some species previously assigned to *Obelia* are removed to allied genera. Although an attempt has been made to consider all described hydroid species, only the more important usages of the name of each have been cited. Full reference lists are already available in the works of Bedot and in abstracting journals.

The taxonomic status of all of the numerous species described from the medusa generation remains problematical. The difficulties outlined by Russell (1953) and Kramp (1961) still remain, and further rearing work may be necessary before the hydroid and medusa species can be related. References to species described from the medusa before 1910 were provided by Mayer (1910) and Bedot, while those described between then and 1959 were listed by Kramp (1961).

The material examined during the present study was drawn mainly from the collections of the British Museum (Natural History). The figures were prepared with the aid of a camera lucida.

GENERIC DIAGNOSIS AND IDENTIFICATION OF THE HYDROID STAGE

Genus *OBELIA* Péron & Lesueur, 1810a¹

Sertularia Linnaeus, 1758 : 807 (part).

Medusa : Slabber, 1769 : 67, pl. 9, figs 5-8 (part) ; Slabber, 1775 : 40, pl. 9, figs 5-8 (part) ; Modeer, 1791 : 25 (part).

Obelia Péron & Lesueur, 1810a¹ : 355 ; Oken, 1815 : 115, pl. 5, fig. 3 ; Deshayes & Edwards, 1840 : 170-171 ; McCrady, 1857 : 197-198, pl. 11, figs 5-7 ; Hincks, 1868 : 146 (part) ; Fraser, 1937 : 82 ; Fraser, 1944 : 151 ; Russell, 1953 : 296 ; Naumov, 1960 : 260 (part) ; Naumov, 1969 : 281 (part) ; [non *Obelia* : Lamouroux, 1821 : 81 ; Deshayes & Edwards, 1836 : 245-246 ; Michelin, 1847 : 321 ; = Bryozoa (d'Orbigny, 1853 : 751 ; Gregory, 1909 : 47 ; Buge, 1951 : 464)].

Laomedea Lamouroux, 1812 : 184 (part) ; Johnston, 1847 : 101 (part) ; Kramp, 1935 : 106 (part).

Slabberia Oken, 1815 : 828 (rejected work, Opinion 417, International Commission on Zoological Nomenclature ; Benthem Jutting, 1970 : 60).

Campanularia Lamarck, 1816 : 112-113 (part).

Thaumantias : Forbes, 1848 : 41 (part).

Eucope Gegenbauer, 1856 : 241 (part) ; [syn. nov.].

Schizocladium Allman, 1871 : 18.

Obelaria Haeckel, 1879 : 173 (nom. nov. pro hydroid stage of *Obelia*).

Obeletta Haeckel, 1879 : 173 ; [syn. nov.].

Obelissa Haeckel, 1879 : 175 ; [syn. nov.].

Monosklera von Lendenfeld, 1885b : 910.

¹ See footnote on facing page.

TYPE SPECIES. *Obelia sphaerulina* Péron & Lesueur, 1810a¹ (nom. nov. pro *Medusa marina* Slabber, 1769); by monotypy; for nomenclatural purposes taken as conspecific with the hydroid *O. dichotoma* (Linnaeus, 1758) (van der Hoeven, 1862 : 280; Russell, 1953 : 297), not *O. geniculata* (Linnaeus, 1758) as proposed by Naumov (1960 : 260; 1969 : 281).

DIAGNOSIS. Colonial Campanulariidae (sensu Russell, 1953) with free medusae. Polyp generation forming upright colonies, branched or unbranched, variably flexuose; internodes annulated proximally, supporting hydrothecal pedicel on distal lateral process. Hydrotheca bell-shaped, hydranth with prominent spherical hypostome. Gonotheca inverted cone-shaped, usually with raised tubular aperture, occasionally simply truncate. Medusa umbrella flat, eversible, mesogloea thin; mouth of manubrium 4-sided, lacking tentacles; marginal tentacles 16+ on release, numerous in adult; gonads 4, spherical, on radial canals.

REMARKS. This restricted diagnosis agrees with that of Fraser (1937, 1944) in excluding from the genus species with no medusa generation (accommodated in the genera *Campanularia* Lamarck, 1816, and *Gonothyrea* Allman, 1864) and also those in which the medusa has only 4 tentacles on release and which, when sexually mature, has a hemispherical umbrella (referred to the genus *Clytia* Lamouroux, 1812). There seems little justification in synonymizing the first two genera plus *Laomedea* Lamouroux, 1812, with *Obelia* as has been proposed by Naumov (1960, 1969). The appearance of the adult medusa of *O. bidentata* Clarke, 1875, is as yet unrecorded, but the characters of its young stages and of the hydroid fall within the above diagnosis.

The polyphyletic genus *Medusa* Linnaeus (1758 : 659) was disbanded by Péron & Lesueur (1810a) who assigned the originally included species to other genera. No species of *Obelia* was included in the original scope of *Medusa*, however, and Péron & Lesueur were justified in forming the genus *Obelia* to accommodate *Medusa marina* Slabber (1769). They also provided a new trivial name for the species, calling it *Obelia sphaerulina*.

d'Orbigny (1853 : 684, 751) cited earlier uses of *Obelia* by Péron in 1803 and 1804, but gave no bibliographic information. Biographies about Péron (Alard, 1811a, b; Audiart, 1855; Girard, 1857) do not list any publication by him in 1803, while Péron's 1804 papers (Péron, 1804a-f) contain no mention of *Obelia*. It seems that d'Orbigny was mistaken in giving these dates and that the name *Obelia* was not introduced until 1810, by Péron & Lesueur.

The genus *Laomedea* Lamouroux, 1812 : 184 was proposed to accommodate two species, *Sertularia dichotoma* Linnaeus, 1758, and *S. spinosa* Linnaeus, 1758. The first-named had, however, previously been removed from *Sertularia* under the name *Obelia sphaerulina* Péron & Lesueur, 1810a, while the second species is currently referred to the bryozoan genus *Vesicularia* Thompson, 1830 (Prenant & Bobin,

¹ Although dated 1809, Péron & Lesueur's paper was not published until January 1810 (Sherborn, 1929 : 4455). They later published a second designation of *Obelia*, dated May 1810, but this work was largely a reprint of part of the earlier paper (Péron & Lesueur, 1810b). A footnote in the first paper states that the plates did not appear with it, and although Lesueur (1811) later published some plates, those from the 1810a paper apparently remain unpublished.

1956 : 276). *S. dichotoma* Linnaeus, 1758, is here selected as type species of the genus *Laomedea* which can thus be considered a junior synonym of *Obelia*. The next available name in place of *Laomedea* auct. appears to be *Campanularia* Lamarck, 1816, which originally included the four species *Sertularia verticillata* Linnaeus, 1758, *S. volubilis* Linnaeus, 1758, *S. syringa* Linnaeus, 1767, and *S. dichotoma* Linnaeus, 1758. Although Nutting (1915 : 28) made *Sertularia verticillata* genotype of *Campanularia*, Naumov (1960 : 249) later nominated *S. volubilis* Linnaeus, 1758 (*not sensu* Ellis & Solander, 1786), as type-species of *Campanularia* and made *Sertularia verticillata* genotype of a new genus, *Verticillina* Naumov, 1960 : 269. Millard (1966 : 477) commented on this confusion and nominated *S. volubilis sensu* Ellis & Solander, 1786 : 51 as type-species of *Clytia* Lamouroux, 1812 : 184. She showed the correct identification of this type-species to be *Medusa hemisphaerica*¹ Linnaeus, 1767 : 1098. However, this species had previously been nominated type-species of the medusoid genus *Thaumantias* Eschscholtz, 1829 : 102, by Forbes (1848 : 41) and *Thaumantias* can be regarded a junior objective synonym of *Clytia*. The status of these genera and their genotypes will be elucidated further by reference to the International Commission on Zoological Nomenclature.

The availability of the generic name *Eucope* Gegenbauer (1856) was discussed by Rees (1939).

The genus *Schizocladium* Allman (1871) was regarded as a junior synonym of *Obelia* by Bedot (1910 : 470). The sole included species is reduced to a synonym of *Obelia dichotoma* in the present review (p. 272).

The genus *Obelaria* Haeckel (1879) was proposed as a *nom. nov.* for the hydroid stage of *Obelia*, of which it is a junior objective synonym, as recognized by Bedot (1912 : 326). The two subgenera *Obeletta* Haeckel (1879) and *Obelissa* Haeckel (1879) were introduced to accommodate taxa defined from the medusa stage. Although thus outside the scope of the present survey they nevertheless at present seem superfluous and can be regarded as junior synonyms of *Obelia*.

The genus *Monosklera* von Lendenfeld, 1885b : 910, was synonymized under *Obelia* by Bedot (1916 : 152). The sole included species is regarded as a synonym of *Obelia geniculata* in the present review (p. 273), following Vanhoffen (1910).

Three species are recognized from the hydroid stage, *O. bidentata* Clarke, 1875, *O. dichotoma* (Linnaeus, 1758) and *O. geniculata* (Linnaeus, 1758). They can usually be identified using the characters shown in Table 1, but occasional specimens occur with characters apparently intermediate between *O. dichotoma* and *O. geniculata*. Usually such specimens are examples of *O. dichotoma* with a slight thickening of the internodal perisarc, and can nevertheless be identified from the characters shown.

¹ Although this species name has been attributed to Gronovius (1760 : 38), his usage was not strictly binominal (Millard, 1966 : 477).

TABLE I
Identification characters of the hydroid stage of *Obelia*

SPECIES	HYDROTICAL RIM	ASYMMETRIC THICKENING OF INTERNODAL PERISARC	GROWTH HABIT	SUBSTRATE*
<i>O. bidentata</i>	Bimucronate or cusped (Fig. 2)	Absent (Fig. 2)	Mature colonies polysiphonic at base, numerous monosiphonic side- branches ; up to c. 350 mm	Probably usually on inert solid substrates and sand
<i>O. dichotoma</i>	Even, sinuous or castellated (Fig. 4)	Absent (Fig. 3)	Usually monosiphonic, much branched, up to c. 350 mm	Usually on animal or inert substrates, less often on algae
<i>O. geniculata</i>	Even (Fig. 5)	Present (Fig. 5)	Monosiphonic ; usually unbranched ; up to c. 40 mm	Usually on brown algae, rarely on animal or inert substrates

* See also the remarks on page 259.

MORPHOLOGICAL AND OTHER VARIATIONS

THE large number of species of *Obelia* described from the hydroid stage reflects the high degree of morphological variation present. Although between-colony variation is readily apparent and many characters are inconstant in expression, nevertheless such characters have been freely used in diagnosing new species. That much variation is phenotypic has long been suspected (Mayer, 1910; Hammett, 1943) but does not seem to have been given due attention in systematic accounts of the genus. All of the new synonymies proposed here result from the adopting of wider specific limits to take account of this variation. The characters used in defining the specific limits are now discussed.

COLONY SIZE. Crowell & Wyttenbach (1957) indicated that there are probably no endogenous factors operating to limit colony-size in *Campanularia flexuosa* (Hincks, in Alder, 1856), and it would seem likely that this also holds in *Obelia*. It follows that colony-size is probably of little or no systematic value. They suggested that colonies of *C. flexuosa* continue their apical growth until natural breakage occurs. It is relevant that the long colonies referred to *O. longissima* by some authors (pp. 256-266) are found in places of limited wave-action, such as broad estuaries [the late D. N. Huxtable (personal communication); personal observation], while shorter colonies hitherto regarded as more typical of *O. dichotoma* occur intertidally and sublittorally where wave-action is greater. Colonies of intermediate lengths occur and on present evidence it appears that colony-size in *O. dichotoma* s. lat. is related to wave-action. The status of *O. longissima* is discussed further below (p. 271).

O. geniculata colonies at a single locality in Massachusetts were usually shorter than 25 mm (Hammett, 1943). Ralph (1956), however, demonstrated a correlation between length and latitude in populations between 35° S and 41° S around New Zealand. Cold-water specimens were up to 40 mm long, while those from the warmest places measured only 5 mm. Later Ralph & Thomson (1968) showed that in Wellington harbour colonies formed in the austral winter were longer than those formed in the summer. Nevertheless, it appears that variation in colony-size in *O. geniculata* is less than in *O. dichotoma*. Information on *O. bidentata* is apparently lacking.

MONOSIPHONIC VERSUS POLYSIPHONIC STEMS. Old stems of *O. bidentata* are invariably polysiphonic, those of *O. dichotoma* are usually monosiphonic and those of *O. geniculata* always so.

BRANCHING OF COLONY. Several species of *Obelia* have been proposed on the basis of the pattern of branching of the colonies. However, this appears not to be correlated with other morphological features. Similarly the length of the branches seems unimportant. The influence of habitat on branching is poorly documented, but Ralph & Thomson (1968) reported that low temperatures induced branching in *O. geniculata*. Occasional dichotomously branched specimens occur in *O. dichotoma*, but it is questionable whether such specimens are truly dichotomous.

INTERNODES. Inter-colony variation occurs throughout the genus in internode length, breadth, length : breadth ratio, curvature, amount of asymmetric internal perisarc thickening, angle of flexure and number of annulations. Of these only the

amount of perisarc thickening seems to have systematic value, being pronounced and asymmetric (although variable) in *O. geniculata* and usually slight and symmetrical in the other two species. Occasional specimens of *O. dichotoma* occur in which the internodal perisarc is slightly thickened on one side, but such specimens can be identified by their hydrothecae. Asymmetric internodal thickening is further discussed below (pp. 271, 277).

DARKENING OF PERISARC. In large colonies of *O. dichotoma* darkening of the internodal perisarc proceeds with age, older parts being dark brown, grading to brown, horn-coloured or transparent in younger parts of the colony. Colonies of *O. geniculata* do not become so dark, while the limited material of *O. bidentata* available suggests that no darkening occurs. Histochemical studies by Knight (1970) showed that in the normal perisarc tanning process of *Campanularia flexuosa* several of the biochemical precursors of melanin are formed and it is possible that this is the dark pigment in *O. dichotoma*.

HYDROTHERCA. Many hydrothecal characters appear to be systematically sound, and they are here regarded as important in defining specific limits within the genus. The hydrothecal rim may be bimucronate or mucronate as in *O. bidentata* (Fig. 2), even, sinuous or castellate as in *O. dichotoma* (Fig. 4) or invariably even as in *O. geniculata* (Fig. 5). The greater variability shown by *O. dichotoma* is not understood, but colonies otherwise similar may differ in having one type of rim or another. The factors involved in the rupture of the embryonic operculum and the consequent formation of the hydrothecal rim are only partly known (Knight, 1965) and it would seem unwise to attach systematic importance to rim-variation until more is known of the factors responsible.

The shape of the hydrotheca appears to be variable in length : breadth ratio, in the angle between the sides as seen in median vertical section and in the degree to which the basal region is curved inwards. Hydrothecae of *O. bidentata* are tubular with a curved basal region while those of *O. geniculata* usually have walls curved throughout their length (Figs 2, 5). Those of *O. dichotoma* are more variable, being tubular to conical (Fig. 4), with or without a curved basal region. A variable amount of thickening of the basal region of the hydrothecal wall occurs in *O. geniculata* but apparently not in the other two species.

The possession of an oblique hydrothecal diaphragm has been used to delimit species otherwise resembling *O. dichotoma*, but it appears to be a variable character and such species are not here regarded as valid (see p. 272). In *O. geniculata*, however, the diaphragm is always transverse while in *O. bidentata* it is always oblique. It has been noted that oblique diaphragms seen in optical section can, from certain angles, appear transverse (Mammen, 1965).

HYDROTHERCAL PEDICEL. Although the number of annulations of the hydrothecal pedicel has been reported as constant at 4–6 in *O. geniculata* (Hammett, 1943), in *O. dichotoma* the number varies between the approximate limits 2–10 and in *O. bidentata* between 3–26 (Mammen, 1965). In both there is often a smooth central portion. There seems to be no indication at present whether this variation is phenotypic or genotypic.

GONOTHECA. Gonotheca shape is similar in the three species and with the exception of the terminal region is approximately constant. In *O. bidentata* and to a lesser extent in *O. dichotoma* gonothecae with apparently truncate ends have been described, there being only a trace of a raised central aperture (Fig. 2; pp. 263–264).

NEMATOCYSTS. Previous work, and also that reported here, suggests that nematocysts do not provide useful specific criteria in *Obelia*.

a. *O. dichotoma* and *O. geniculata*. The lengths of fresh, undischarged microbasic mastigophores from living hydranth tentacle-tips of the two species are shown in Table 2. The sizes varied to the extent that the range of measurements obtained

TABLE 2

Measurements of undischarged nematocysts from the tips of hydranth tentacles of *Obelia* spp., $\pm 0.2 \mu\text{m}$

SPECIES	LOCALITY	LENGTH			WIDTH	REMARKS
		<i>n</i>	$\bar{x}$	S.E.		
<i>O. geniculata</i>	Cornwall (1973.9.24.2)	22	6.8	0.0826	All 2.0	Fresh
	Cornwall (1973.9.24.3)	20	6.9	0.0444	All 2.0	Fresh
<i>O. dichotoma</i>	Devon (1973.7.23.1)	20	7.3	0.0857	All 2.0	Fresh
	Devon (1973.9.24.4)	20	6.7	0.0466	All 2.0	Fresh, specimen resembled <i>O. longissima</i> sensu Alder
<i>O. bidentata</i>	Norfolk (1953.11.16.1)	10	5.6	0.0897	All 1.5	Formalin-preserved

n = number in sample, $\bar{x}$ = mean, S.E. = standard error. 'Fresh' nematocysts are those taken from living hydranths.

from one species fell within the range recorded from the other. Application of Student's *t*-test showed nematocyst-length to be similar in the two *O. geniculata* populations ($p < 0.001$), but dissimilar in the two groups of *O. dichotoma* ($p > 0.32$).

Two types of nematocyst have previously been recorded from *O. geniculata*. Ito & Inoue (1962) reported microbasic mastigophores (measuring $4.9\text{--}5.2 \mu\text{m} \times 1.3\text{--}1.5 \mu\text{m}$ undischarged) from the hydranths, while Weill (1934b) identified basitrichous isorhizas (length $5 \mu\text{m}$) from the tentacles of both hydranth and medusa. Only the latter type has been recorded from *O. dichotoma*, from the medusa (Westfall, 1966, as *O. longissima*; measurements not stated). Thus the present recording of microbasic mastigophores in *O. dichotoma* is new. However, the identification of the two kinds of nematocyst depends on the presence or absence of a butt (Fig. 1), a feature which can be ascertained only in discharged capsules (Weill, 1934a). Maybe a butt is not always present. It is certainly so small in *Obelia* as to be difficult to observe with the light microscope. Possibly more extensive observations on *Obelia* from various localities will explain the reported occurrence of both types.

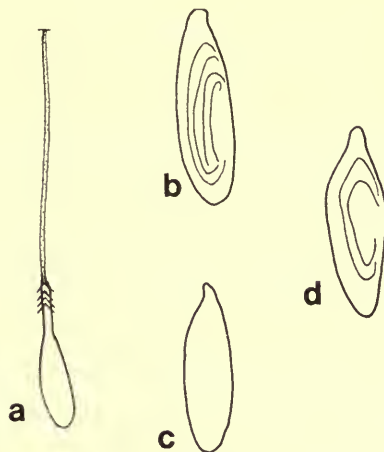


FIG. 1. *Obelia geniculata*. Microbasic mastigophores from live hydranths. SW. England (1973.9.24.2). (a) Discharged. Capsule, $7\text{ }\mu\text{m}$; butt, $6\text{ }\mu\text{m}$; barbs $c. 1.5\text{ }\mu\text{m}$; thread, $63\text{ }\mu\text{m}$ (not all shown). Note distinct butt at base of thread. (b-d) Undischarged, different scales. Lengths, $6.8\text{ }\mu\text{m}$; breadths, $2\text{ }\mu\text{m}$ (see Table 2 for standard error). One side is slightly flatter than the other, and the tip of the capsule inclines to one side.

b. *O. bidentata*. Measurements of undischarged nematocysts from the tentacle-tips of formalin-preserved hydranths are shown in Table 2, living material being unobtainable. The preserved nematocysts at least were similar in size to those from live hydranths of the other two species. Identification was not attempted as no discharged nematocysts were seen, but the undischarged ones closely resembled those of the other species and may prove to be of the same kind.

BIOLUMINESCENCE. Although Hincks (1868) reported bioluminescence only in *O. geniculata*, it has now been reported in all three *Obelia* hydroids (Morin & Cooke, 1971).

SUBSTRATE. *O. geniculata* has been widely recorded on the blades of laminarian and fucoid algae, whereas *O. dichotoma* occurs usually on animal and inert substrates and less frequently on algae (Hincks, 1868; Hammett, 1943; Barrett & Yonge, 1958; Fey, 1969). Manton (1942) examined the attachment of the hydrorhiza of *Obelia* sp. to an unspecified substrate, and found that the coenosarc was not involved. Sections cut during the present study along the stolons of *O. geniculata* (1973.7.23.2-3) and into the algal substrate showed no tissue connections between hydroid and alga. It seems likely, therefore, that the growth-form of *O. geniculata* is not related to substrate. The occasional occurrence of each species on the substrate more usual for the other is additional evidence that substrate does not influence morphology. The substrate-preference of *O. bidentata* is less well known but is said to be for inert solid substrates and also sand (Vervoort, 1946a) to which neither of the other two species attaches directly.

MEDUSA GENERATION. The medusae of the three hydroid species, although variable, cannot at present be distinguished (see pp. 278-279).

***Obelia bidentata* Clarke, 1875**

(Fig. 2)

- Obelia bicuspidata* Clarke, 1875 : 58, pl. 9, fig. 1 ; Bedot, 1912 : 326 ; Nutting, 1915 : 80, pl. 20, figs 5-6 (= *O. bidentata* Clarke) ; Bedot, 1916 : 160 ; Bedot, 1918 : 195 ; Bedot, 1925 : 298-299 (= *O. bidentata* Clarke) ; Fraser, 1944 : 153-154, pl. 27, fig. 125 (= *O. bidentata* Clarke ; *L. spinulosa* var. *minor* Leloup) ; Deevey, 1950 : 343 (= *O. oxydentata* Stechow ; *L. spinulosa* var. *minor* Leloup) ; Leloup, 1952 : 157, fig. 89 (= *C. spinulosa* Bale) ; Vannucci, 1954 : 108-110, pl. 2, figs 2-7, 9-10 (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *O. bifurca* Hincks ; *Obelia* sp. Clarke ; *O. oxydentata* Stechow) ; Millard, 1958 : 174 ; Mammen, 1965 : 11-13, figs 37-38 ; Millard & Bouillon, 1973 : 56 (= *G. longicyatha* : Jarvis).
- Obelia bidentata* Clarke, 1875 : 58-59, pl. 9, fig. 2 ; Pictet, 1893 : 25-26, pl. 1, figs 20-21 ; Jaderholm, 1904a : 270-271 (= *O. bicuspidata* Clarke) ; Jaderholm, 1904b : vii (= *O. bicuspidata* Clarke) ; Jaderholm, 1905b : 17 ; Mayer, 1910 : 254 [= *O. bicuspidata* Clarke ; ? = *O. austrogeorgiae* Jaderholm ; (see below, p. 280)] ; Bedot, 1912 : 326 ; Billard, 1912 : 463, fig. 2 (= *O. bicuspidata* Clarke) ; Bedot, 1916 : 160 ; Bedot, 1918 : 195 ; Kramp, 1961 : 162 ; Teissier, 1965 : 16 ; Fey, 1969 : 393.
- ? *Obelia longicyatha* Allman, 1877 : 10, pl. 7, figs 4-5 ; (see below, p. 264).
- Campanularia spinulosa* Bale, 1888 : 756-757, pl. 12, figs 5-7.
- Obelia andersoni* Hincks, 1889 : 132-133, pl. 12, figs 2-4 ; Thornely, 1904 : 113 ; Ritchie, 1910 : 810 ; [syn. nov.].
- Obelia bifurca* Hincks, 1889 : 133, pl. 12, fig. 1 ; Mayer, 1910 : 494 ; [syn. nov.].
- Gonothyrea longicyatha* Thornely, 1899 : 454-455, pl. 44, figs 4, 4a (non *O. longicyatha* Allman, 1877).
- Obelia corona* Torrey, 1904 : 14, figs 5-6 ; Nutting, 1915 : 79, pl. 20, figs 1-2 ; [syn. nov.].
- Obelia* sp. Clarke, 1907 : 10-12, pl. 5, figs 5-7.
- Obelia bifurcata* Thornely, 1908 : 81-82, pl. 9, fig. 2 (nom. nov. pro *O. bifurca* Hincks).
- Laomedea bidentata* : Babič, 1913 : 284-286, fig. 1 (= *O. bicuspidata* Clarke).
- Obelia multidentata* Fraser, 1914 : 154, pl. 17, fig. 56 ; Fraser, 1937 : 89-90, pl. 18, fig. 93 ; [syn. nov.].
- Obelia oxydentata* Stechow, 1914 : 131-132, fig. 7 (nom. nov. pro *Obelia* sp. Clarke) ; Stechow, 1919 : 50 ; Vannucci Mendes, 1946 : 555-556, pl. 2, fig. 22 ; Hirohito, 1969 : 9-10, fig. 8a-b.
- Gonothyrea bicuspidata* : Stechow, 1919 : 50-51 (= *O. bidentata* Clarke ; *G. longicyatha* Thornely) ; Vannucci Mendes, 1946 : 556-557, pl. 3, fig. 23 [= *O. bidentata* Clarke ; ? = *O. austrogeorgiae* : Nutting, 1915 ; (see below, p. 280)].
- Obelia longa* Stechow, 1921a : 221-223, fig. 1 ; Stechow, 1925 : 436-437, figs 12b, 13 ; [syn. nov.].
- Gonotha longicyatha* (sens. Thornely) : Jarvis, 1922 : 336.
- Clytia longitheca* Hargitt, 1924 : 484, pl. 3, fig. 9 ; [syn. nov.].
- Obelia longitheca* Hargitt, 1924 : 484-485, pl. 3, fig. 10 ; [syn. nov.].
- Obelia attenuata* Hargitt, 1924 : 486, pl. 3, fig. 11 ; [syn. nov.].
- Obelia spinulosa* : Billard, 1927 : 333-334, fig. 2.
- Laomedea bicuspidata* var. *picteti* Leloup, 1932 : 151-153, pl. 17, figs 4, 4d, text-fig. 19.
- Laomedea spinulosa* var. *minor* Leloup, 1932 : 155-158, pl. 17, figs 6, 6a, text-figs 24-25.
- Laomedea bicuspidata* : Hummelinck, 1936 : 53-57, fig. 8a-v (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *G. longicyatha* Thornely ; *Obelia* sp. Clarke ; *O. oxydentata* Stechow ; *L. bicuspidata* var. *picteti* Leloup ; *L. spinulosa* var. *minor* Leloup) ; Vervoort, 1946a : 298-300, fig. 132a-f (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *G. longicyatha* Thornely ; *O. oxydentata* Stechow) ; Vervoort, 1946b : 344-345, fig. 10a-b ; Hamond, 1957 : 312-313, figs 20-21 ; Vervoort, 1959 : 315 ; Vervoort, 1972a : 92-93, fig. 26d (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *L. spinulosa* var. *minor* Leloup ; *Obelia* sp. Clarke ; *O. oxydentata* Stechow).
- ? *Clytia longicyatha* (sens. Allman) : Fraser, 1944 : 142, pl. 25, fig. 114 ; (see below, p. 264).
- Clytia longicyatha* (sens. Allman) : Rees & White, 1966 : 276.

Laomedea bicuspidata var. *tenuis* Vervoort, 1946b : 345-346, fig. 10c (nom. nov. pro *L. spinulosa* var. *minor* Leloup).

? *Laomedea longicyatha* (sens. Allman) : Vervoort, 1946b : 343-344.

Laomedea (Obelia) bicuspidata : Vervoort, 1968 : 19-21, fig. 7 (= *O. bidentata* Clarke ; *C. spinulosa* Bale ; *Obelia* sp. Clarke ; *C. spinulosa* var. *minor* Leloup).

Laomedea (Obelia) longicyatha (sens. Allman) : Vervoort, 1968 : 21-22, fig. 8 ; Vervoort, 1972a : 93.

non *Clytia longicyatha* (sens. Allman) : Pictet, 1893 : 28-29, pl. 2, figs 22-23 (= *Clytia* sp., see below, p. 264).

TYPE LOCALITY. Greenport, Long Island, New York, U.S.A., on wharf piles (Clarke, 1875).

DIAGNOSIS. *Obelia* hydroid usually with branched, erect hydrocaulus ; polysiphonic basally, internodes straight, narrow, lacking internal thickening of perisarc and not usually strongly tanned ; rim of hydrotheca with a variable number of cusps, usually bimucronate.

DESCRIPTION. Mature colony comprising several erect, sometimes flexuose, polysiphonic stems up to 350 mm, alternate lateral hydrocauli bearing the hydrothecae ; basal hydrorhiza on sandy substrates a tangled mass of stolons. Lateral

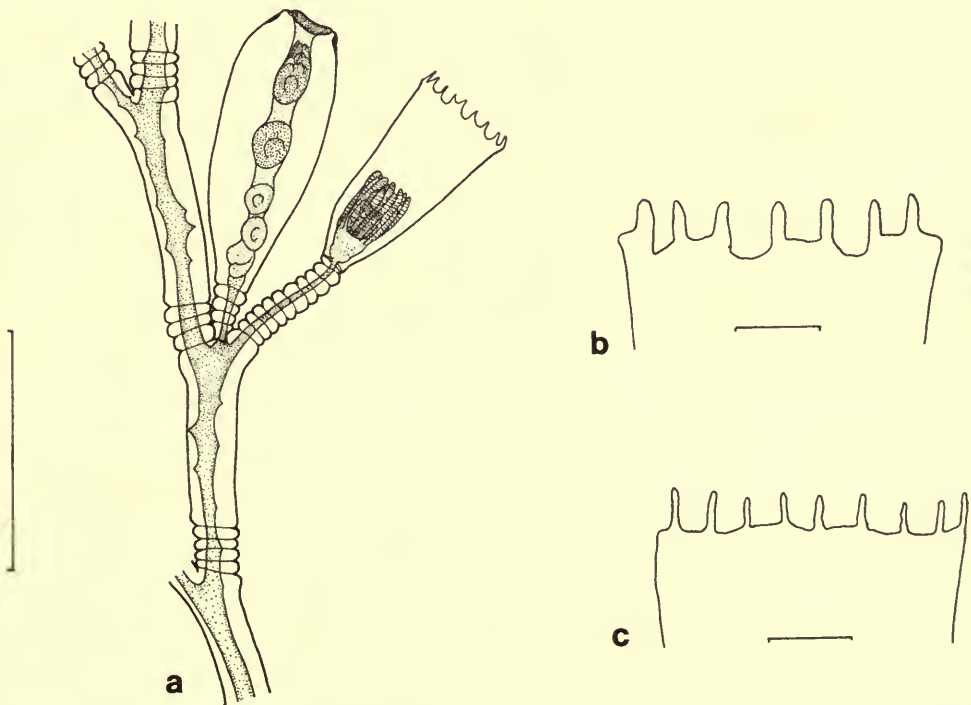


Fig. 2. *Obelia bidentata*. (a) Nigeria (1966.10.6.1). Part of hydrocaulus and ripe gonotheca with aperture only slightly raised. Scale = 500 μ m. (b) Sierra Leone (1966.10.7.5). Bimucronate hydrothecal rim slightly irregular. Scale = 50 μ m. (c) Nigeria (1966.10.8.117). Hydrothecal rim with indentations of similar depth (? atypical). Scale = 50 μ m.

hydrocauli delicate, slightly flexuose; internodes long, annulated proximally, with lateral process distally to which hydrothecal pedicel is attached. Pedicel ringed throughout or with central smooth portion; hydrotheca 1-3 times long as broad, bell-shaped, slightly asymmetric, sometimes having folds in the hydrothecal wall between cusps running proximally from the rim; diaphragm oblique (can appear transverse in optical section); rim with 10-20 bimucronate cusps (rarely, simply cusped; Fig. 2a-c); hydranth undescribed. Gonotheca usually an inverted cone with raised aperture; occasionally truncated with broad aperture, lacking raised structure. Measurements - see Table 3.

TABLE 3
Measurements of the hydroid stage of *Obelia bidentata* in μm

	NIGERIA (1966.10.6.1; Fig. 2a)	SIERRA LEONE (1966.10.7.8)	SOUTH YEMEN (1966.11.15.2)	NORFOLK, ENGLAND (1953.11.16.1)
HYDROTHECA				
Length (diaphragm to tips of cusps)	400-470	340-490	320-430	380-430
Breadth at rim	210-270	120-230	180-280	200-220
HYDROTHECAL PEDICELS				
Length	070-240	070-580	060-410	070-240
INTERNODES				
Length	450-680	400-570	320-480	480-710
Maximum breadth	080-130	070-080	070-090	080-120
Length/breadth ratio	c. 6	5-6	5-6	5-6
GONOTHECA				
° Length	550-600	—	—	—
Maximum breadth	220-260	—	—	—

MATERIAL EXAMINED. *Atlantic Ocean* - Greenport, Long Island, New York, U.S.A., 5 August 1874, several infertile hydrocauli in spirit, **syntypes**, Yale Peabody Museum of Natural History no. 3119. Thimble Island, Branford, Connecticut, U.S.A., 23 September 1874, three fragments in spirit, **syntypes** of *O. bicuspidata* Clarke, Yale Peabody Museum of Natural History no. 7265.

Hunstanton, Norfolk, England, 26 September 1953, several large colonies in spirit, coll. R. Hamond, 1953.11.16.1¹ (Table 2). Shellness, Isle of Sheppey, Kent, England, strandline, 23 September 1973, two abraded colonies in spirit, coll. P. F. S. Cornelius, 1973.9.24.1.

Zeeland Province, Netherlands, 20 August 1946, several colonies in spirit, Leiden Rijksmuseum van Natuurlijke Historie no. 3687.

Monte Brazil W., Terceira I., Azores, 29 m, 27 July 1959 and August 1959, several colonies in spirit, coll. Imperial College Azores Expedition, 1962.1.15.17, 21 (Rees & White, 1966, as *Clytia longicyatha*; see p. 264).

¹ Registered numbers of this format refer to British Museum (Natural History) collections, unless otherwise stated.

Trinidad, West Indies, August 1966, three microslides of fragments, coll. J. H. Wickstead, 1966.11.11.1.

Port Harcourt, Nigeria, 11 July – 14 November 1957, 26 microslides of fragments, coll. H. G. Stubbings, 1966.10.8.14, 31, 44, 55, 56, 58, 70, 74, 92, 93, 95, 112, 117, 119, 120, 124 (Fig. 2c). Lagos, Nigeria, 1957, four microslides of fragments, coll. M. B. Hill, 1958.3.1.1–4. Lagos Harbour, Nigeria, January 1959, 1 m, one microslide of fragments, coll. M. B. Hill, 1966.10.6.1 (Fig. 2a).

Bunce Island, Sierra Leone, 19 February 1955, seven microslides of fragments, coll. A. Longhurst, 1966.10.7.5–11 (Fig. 2b).

Indo-Pacific Ocean – Sapper Bay, Aden, South Yemen, 17 August 1966, coll. K. W. England, one microslide of fragments, 1966.11.15.2.

Amoy, China, December 1925, one colony in spirit, coll. C. Ping, 1926.3.17.36.

On Hong Kong to Manilla cable, 20°57' N, 115°23' E, c. 200 m, 21 February 1929, one microslide of fragments, coll. British East India Company, 1929.4.18.20.

OTHER MATERIAL RECORDED. *North Atlantic* – West European waters from Helgoland (Kramp, 1961), Netherlands, Belgium, northern France (Vervoort, 1946a; Leloup, 1952; Teissier, 1965; Fey, 1969); Mediterranean Sea (Vervoort, 1946b), Algeria (Picard, 1955), Azores (Rees & White, 1966), Ghana (Buchanan, 1957), tropical W. Africa (Vervoort, 1959). North American coast from Casco Bay, Maine, south to Caribbean and Panama (Fraser, 1946; Vervoort, 1946b, 1968).

South Atlantic – South American coast from Brazil (Fraser, 1946; Vannucci Mendes, 1946) and near Tierra del Fuego (Vervoort, 1972a).

Pacific – San Francisco Bay (Fraser, 1937, 1946), Hawaii (Vervoort, 1946b), Japan (Hirohito, 1969, as *O. oxydentata*), New Britain Island (Vervoort, 1946b), Port Jackson, New South Wales, Australia (Bale, 1888, as *Campanularia spinulosa*).

Indian Ocean – Several localities off India and Malaya (Vervoort, 1946b; Mammen, 1965), Kerguelen Island (Stechow, 1925, as *O. longa*), Natal (Millard, 1958), Mozambique and Seychelles (Millard & Bouillon, 1973, 1974).

DISTRIBUTION. Continental shelf depths in tropical, sub-tropical and some temperate seas in both northern and southern hemispheres. Records furthest from the equator are Helgoland (54° N), South Georgia and Tierra del Fuego (both 54° S). Reported unrecorded from Argentina (Vervoort, 1972a), New Caledonia (Redier, 1966), Tasmania (Hodgson, 1950), South Australia (Blackburn, 1942), New Zealand and the Chatham Islands (Ralph, 1957, 1961), south and west coasts of the Republic of South Africa (Millard, 1957).

REMARKS. The number of bimucronate cusps on the hydrothecal rim may vary between 10 and 20 (Nutting, 1915; Mammen, 1965), although at any one locality the range of variation is less. Most specimens have alternating deep and shallow notches around the hydrothecal rim but in some the gaps are of almost equal depth and the bimucronate condition is obscured (Fig. 2b–c).

Two kinds of gonothecae have been recorded. The more usual kind is typical of *Obelia*, with a tubular aperture (Nutting, 1915; Hamond, 1957; Hirohito, 1969) while the other is truncated distally and opens directly (Babič, 1913; Fraser, 1937; Mammen, 1965). Possibly a reduced tubular aperture was overlooked by

authors describing a truncate gonotheca. Medusa release was recorded from normal gonothecae by Hamond, while a BM(NH) specimen shows medusae developing within an apparently truncate gonotheca (Fig. 2a).

The two nominal species *O. bicuspidata* and *O. bidentata* were first described on the same page by Clarke (1875). They were synonymized under *O. bidentata* by Jaderholm (1904a, b, 1905a), whose usage as first reviser was followed by Mayer (1910), Billard (1912) and Babić (1913). Nutting (1915), however, used *O. bicuspidata* as the senior synonym, although including Jaderholm's 1904a paper in his synonymy. Since then *bicuspidata* has been used more frequently than *bidentata* but Jaderholm's usage gives *bidentata* priority.

Two varieties of the species have been described. *Laomedea spinulosa* var. *minor* Leloup, 1932, was erected to accommodate forms differing only in the height of the colony. Vervoort (1972a), however, placed var. *minor* Leloup together with *L. bicuspidata* var. *tenuis* Vervoort, 1946b (a new name for Leloup's variety), in the synonymy of *O. bicuspidata*. The second variety, *O. bicuspidata* var. *picteti* Leloup, 1932, was distinguished on specimens with long gonothecae. As such variation is common and has no apparent taxonomic value, the separation is not upheld here.

There is some confusion concerning *Obelia longicyatha* Allman, 1877, and another nominal species of the same name, *O. longicyatha* (Thornely, 1899). The type specimens of neither species could be located. Allman's species, described from infertile material, was said to have long pointed cusps on the hydrothecal rim reminiscent of *Clytia*, to which genus the species has been referred by several authors (references in Fraser, 1944). Nevertheless, the form of the colony as illustrated by Allman equally suggests *O. bidentata*, and the affinities of the species remain unclear. Pictet (1893) referred to Allman's species material with developing medusae clearly not of *Obelia* type and referred his material to *Clytia*. Vervoort (1946b) described under Allman's species material identical with *O. bidentata* except that the hydrothecae were unusually long (900–950 μm). The gonothecae were typical for the species. Vervoort (1968) later described other, infertile, material with hydrothecae nearer in size (580–620 μm) to the measurements given here (320–490 μm) and illustrated an oblique hydrothecal diaphragm characteristic of *O. bidentata*. Vervoort (1972a) subsequently referred another infertile specimen to Allman's species, distinguishing it from *O. bidentata* on the basis of hydrothecal length. However, it seems unclear at present whether or not specimens of such dimensions fall within the range of variation of *O. bidentata*, and the identity of Vervoort's material is problematical. In contrast the material identified with Allman's species by Rees & White (1966) and re-examined here seems identical with *O. bidentata*, having characteristic bimucronate hydrothecal rims and falling within the normal size-range. The other species, *O. longicyatha* (Thornely, 1899), was stated in the original description to have such hydrothecal rims and Stechow (1919) and Hummelinck (1936) justifiably referred it to *O. bidentata*. Jarvis (1922) referred to *Gonotha longicyatha* specimens with bimucronate hydrothecal cusps and truncate gonothecae which seem also to have been typical *O. bidentata*.

Obelia andersoni Hincks, 1889, from the Mergui Archipelago, can be referred to *O. bidentata*. It was originally distinguished on the basis of a sharp demarcation

between the cylindrical side of the hydrotheca and its inward-sloping base. Thornely (1904) found similar material in which there was no sharp demarcation, and the species appears invalid.

The affinities of *O. austrogeorgiae* Jaderholm, 1904b, are discussed on page 280.

MEDUSAE. It has often been established that *O. bidentata* releases a medusa (Hincks, 1889, as *O. andersoni*; Pictet, 1893, as *O. bidentata*; Thornely, 1899, as *Gonothyrea longicyatha*; Billard, 1927, as *O. spinulosa*; Fraser, 1944, as *Clytia longicyatha* sensu Allman; the following, as *O. bicuspidata*: Vervoort, 1946a, b; Vannucci, 1954; Hamond, 1957; Mammen, 1965; and Fey, 1969, as *O. bidentata*). However, the medusae were apparently not recorded as resembling those of the other *Obelia* species until Billard (1927) identified them in the gonotheca. Subsequently Hamond (1957) and Mammen (1965) confirmed the resemblance by observing newly liberated medusae. Adult specimens have not been described and the best available description, of the young stage, is that by Mammen. The young stage at least is very similar to that in the other two species.

Obelia dichotoma (Linnaeus, 1758)

(Figs 3 & 4)

Sertularia dichotoma Linnaeus, 1758: 812; Linnaeus, 1767: 1312 (= *S. longissima* Pallas); Maratti, 1776: 34; Rees, 1819: unpaginated; Dalyell, 1836a: 91-92, 94, fig. 1; Dalyell, 1836b: 84-85, 87, fig. 1.

Sertularia longissima Pallas, 1766: 119-121 (nom. nov. pro *S. dichotoma* Linnaeus).

Sertolare geniculata Cavolini, 1785: 205, pl. 8, figs 1-4 (lapsus pro *Sertularia geniculata* Linnaeus).

Laomedea dichotoma: Lamouroux, 1812: 184; Johnston, 1838: 150-151, pl. 22, figs 1-2 (= *Sertularia longissima* Pallas); Johnston, 1847: 102-103, 119, pl. 26, figs 1-2 (= *S. longissima* Pallas); Alder, 1857: 121 (= *Campanularia gelatinosa*: van Beneden); Hincks, 1861: 258.

Sertularia geniculata: Sprengel, 1813: 95-97, pl. 8, figs 3-4.

Campanularia dichotoma: Meyen, 1834: 193-195, pl. 30, figs 1-4, pl. 31, fig. 1; [non *C. dichotoma*: Grant, 1826: 150-156 (= *Laomedea flexuosa* Hincks, in Alder, 1856)].

Campanularia maior Meyen, 1834: 196-197, pl. 32, figs 1-4; Bedot, 1905: 53; [syn. nov.].

Campanularia brasiliensis Meyen, 1834: 198, pl. 32; Nutting, 1915: 77, pl. 18, figs 8-9; [syn. nov.].

Campanularia cavolinii Deshayes & Edwards, 1836: 133 (nom. nov. pro *Sertularia geniculata*: Cavolini); [syn. nov.].

Campanularia caulini Chiaje, 1841: 143 (unjustified emendation of *C. cavolinii* Deshayes & Edwards).

Sertularia cavolinii: Kölliker, 1843: 81; [syn. nov.].

Campanularia gelatinosa: van Beneden, 1844: 33-34, pls 1-2; Maitland, 1876: 13 (= *Obelia sphaerulina* Péron & Lesueur, 1810a); (see p. 279).

Laomedea longissima: Alder, 1857: 121-122; Hincks, 1861: 259.

Obelia commissuralis McCrady, 1857: 197-198, pl. 11, figs 5-7; Agassiz, 1862: 315-321, pls 33-34, figs 10-21; Agassiz, 1865: 91-92, figs 134-135 (= *Laomedea dichotoma*: Leidy; *L. gelatinosa*: Gould, Stimpson); Norton, 1896: 291-296, figs 1-12; Nutting, 1915: 83, pl. 21, figs 1-5; Berrill, 1949: 235-264; Vannucci, 1951: 80-81, pl. 2, figs 8-9; Mammen, 1965: 14-15, fig. 41 (? = *O. hyalina* Clarke); [syn. nov.].

Laomedea divaricata McCrady, 1857: 195-196; Agassiz, 1865: 91.

Eucope parasitica Agassiz, 1865: 87; [syn. nov.].

- Eucope pyriformis* Agassiz, 1865 : 88-89 ; Mayer, 1910 : 247 (? = *Laomedea divaricata* McCrady) ; [syn. nov.].
- Eucope articulata* Agassiz, 1865 : 89-90, figs 130-131.
- Campanularia flabellata* Hincks, 1866 : 297 (nom. nov. pro *C. gelatinosa* : van Beneden).
- Obelia longissima* : Hincks, 1868 : 154-155, pl. 27 (= *Campanularia gelatinosa* : van Beneden) ; Russell, 1953 : 303, fig. 185c ; Naumov, 1960 : 263-264, figs 149-151 ; Naumov, 1969 : 284, figs 149-151.
- Obelia dichotoma* : Hincks, 1868 : 156-157, pl. 28, fig. 1, 1a-b ; Mayer, 1910 : 245-246, 248, pl. 30, figs 1-2 ; text-figs 125-127 (= *Eucope articulata* Agassiz ; *O. sphaerulina* : Haeckel ; ? *O. australis* von Lendenfeld ; *O. rhunicola* Billard) ; Bedot, 1925 : 301 (= *O. rhunicola* Billard) ; Russell, 1953 : 303, fig. 185b ; Millard, 1966 : 483 (= *O. dubia* : Vanhoffen ; *Campanularia obtusidens* Jaderholm).
- Obelia flabellata* : Hincks, 1868 : 157-158, pl. 29 ; Nutting, 1915 : 84-85, pl. 22, figs 3-4 (= *O. plana* : Mayer ; see footnote, p. 271).
- Obelia plicata* Hincks, 1868 : 159, pl. 30, figs 1, 1a ; Nutting, 1915 : 78, pl. 19, figs 5-6 ; [syn. nov.].
- Schizocladium ramosum* Allman, 1871 : 18-21, pl. 2, figs 1-8 ; [syn. nov.].
- Obelia pygmaea* Coughtrey, 1876 : 25, pl. 3, fig. 3 ; Ralph, 1957 : 832 (? = *O. longissima* (Pallas)) ; [syn. nov.].
- Obelia hyalina* Clarke, 1879 : 239, 241-242, pl. 4, fig. 21 (non *Gonothyrea hyalina* Hincks, 1866).
- Obelia adelungi* Hartlaub, 1884 : 164-165, text-fig. 1 ; [syn. nov.].
- Obelia helgolandica* Hartlaub : 1884 : 165-167, text-fig. 2 ; [syn. nov.].
- Obelia australis* von Lendenfeld, 1885a : 604, 630 ; Bale, 1888 : 753-754, pl. 12, figs 1-2 ; Ralph, 1957 : 830, fig. 4a-h ; Mammen, 1965 : 11.
- Obelia angulosa* Bale, 1888 : 752-753, pl. 12, fig. 3 ; Mayer, 1910 : 257 ; [syn. nov.].
- Obelia chinensis* Marktanner-Turneretscher, 1890 : 209-210, pl. 3, figs 6-7 ; Mayer, 1910 : 242 (? = *O. plana* : Haeckel) ; [syn. nov.].
- Obelia arruensis* Marktanner-Turneretscher, 1890 : 210, pl. 3, fig. 8 ; [syn. nov.].
- Obelia nigrocaulus* Hilgendorf, 1898 : 203-204, pl. 17, figs 1, 1a ; Bale, 1924 : 230.
- Obelia gracilis* Calkins, 1899 : 353-354, pl. 3, figs 13, 13a-c, pl. 6, fig. 13d [non *Laomedea gracilis* Sars, 1850 = *Campanularia pelagica* van Breemen, 1905 (Vervoort, 1946a : 285)] ; Nutting, 1915 : 78, pl. 19, figs 2-4 ; Hargitt, 1927 : 504-505 ; Ling, 1938 : 183 ; Blanco, 1967 : 130-134, figs 1-16 ; [syn. nov.].
- Obelia surcularis* Calkins, 1899 : 355, pl. 3, figs 14, 14a-b, pl. 6, fig. 14c ; Nutting, 1915 : 84, pl. 22, figs 1-2 ; [syn. nov.].
- Obelia fragilis* Calkins, 1899 : 355-356, pl. 3, figs 15, 15a-b, pl. 6, fig. 15c ; Nutting, 1915 : 87, pl. 33, fig. 6 ; [syn. nov.].
- Obelia griffini* Calkins, 1899 : 357, pl. 4, figs 18, 18a-c, pl. 6, fig. 18d ; Nutting, 1915 : 87, pl. 23, figs 4-5 ; Vannucci Mendes, 1946 : 552-553, pl. 2, figs 16-17 ; [syn. nov.].
- Obelia rhunicola* Billard, 1901b : 522-523.
- Obelia borealis* Nutting, 1901 : 174, pl. 19, figs 4-6 ; Nutting, 1915 : 85, pl. 22, figs 5-7 ; [syn. nov.].
- Obelia dubia* Nutting, 1901 : 174, pl. 20, fig. 1 ; Nutting, 1915 : 77, pl. 19, fig. 1 ; Mayer, 1910 : 248 (? = *O. dichotoma* : Hincks) ; Vanhoffen, 1910 : 307-308, fig. 27 ; Bedot, 1925 : 302 (= *Campanularia obtusidens* Jaderholm).
- Obelia solowetzkiiana* Schydlovsky, 1902 : 123-125, pl. 3, figs 20-22 (nom. nov. pro *O. flabellata* : Schlater) ; Jaderholm, 1909 : 63 ; [syn. nov.].
- Campanularia obtusidens* Jaderholm, 1905a : 2, pl. 1, fig. 1.
- Obelia congdoni* Hargitt, 1909 : 375-376 (nom. nov. pro *O. hyalina* Congdon) ; [syn. nov.].
- Obelia articulata* : Mayer, 1910 : fig. 126.
- Obelia pyriformis* : Mayer, 1910 : 240, 247, fig. 128 (= *Laomedea divaricata* McCrady).
- Obelia piriformis* Bedot, 1910 : 342 (lapsus pro *pyriformis*).
- Obelia undotheca* Stechow, 1923a : 4 ; Stechow, 1923b : 115-117, fig. O ; [syn. nov.].
- Obelia nodosa* Bale, 1924 : 230, fig. 1 ; Ralph, 1957 : 832, fig. 5i-k ; [syn. nov.].

- Obelia coughtreyi* Bale, 1924 : 230–231, fig. 2 ; [syn. nov.]
Obelia obtusidentata Bedot, 1925 : 302 (lapsus pro *obtusidens*).
Obelia everta Hargitt, 1927 : 505, fig. 4 ; [syn. nov.]
Obelia alternata Fraser, 1938 : 35–36, pl. 8, fig. 38 ; [syn. nov.]
Obelia equilateralis Fraser, 1938 : 36–37, pl. 9, fig. 39 ; Fraser, 1944 : 157, pl. 28, fig. 128 ; [syn. nov.]
Obelia microtheca Fraser, 1938 : 37, pl. 9, fig. 40 ; [syn. nov.]
Obelia tenuis Fraser, 1938 : 38–39, pl. 9, fig. 42 ; [syn. nov.]
Obelia racemosa Fraser, 1941 : 82, pl. 15, fig. 7 ; [syn. nov.]
Obelia irregularis Fraser, 1943 : 77 ; Fraser, 1944 : 162, pl. 29, fig. 132 ; [syn. nov.]
? *Obelia obtusidens* : Fraser, 1944 : 163–164, pl. 29, fig. 134 ; (see p. 272).
Obelia braziliensis Vannucci Mendes, 1946 : 553–555, pl. 2, figs 20–21 (lapsus pro *brasiliensis*).
Obelia biserialis Fraser, 1948 : 213, pl. 24, fig. 6 ; [syn. nov.]
Laomedea (Obelia) dichotoma : Vervoort, 1959 : 315–316.
Laomedea (Obelia) congdoni : Vervoort, 1968 : 23 (= *O. hyalina* Clarke ; *L. sargassi* Leloup).

TYPE SPECIMEN AND TYPE LOCALITY. Ellis, 1755 : 21–22, pl. 12, fig. A, but not fig. a ; coast of SW. England.¹ Location of specimen unknown.

DIAGNOSIS. *Obelia* hydroid usually with branched, flexuose, monosiphonic hydrocauli ; internodes long, straight or slightly curved, without asymmetric perisarc thickening. Perisarc colourless in small specimens ; tanned to a horn-colour, brown or black in large colonies. Hydrothecal pedicels long, ringed, sometimes with smooth central portion. Hydrothecae straight-sided, curving basally, often slightly flared at rim, which may be even, castellate or sinuous, frequently with minute longitudinal folds in the hydrothecal wall.

DESCRIPTION. Main stems of colonies usually monosiphonic, flexuose, 10–350 mm ; racemose hydrocauli with shorter lateral branches ; occasional specimens apparently dichotomous (see p. 256). Main hydrocauli frequently tanned to a horn-colour, often brown or black, darker basally ; internodes long, nodes usually annulated, process supporting hydrothecal pedicel distal (Fig. 3). Hydrothecal pedicel long, annulated throughout or with smooth central portion ; hydrotheca bell-shaped, occasionally flared distally ; length 1–2 times greatest breadth ; rim usually even but often sinuous or castellate (Fig. 4), frequently with minute longitudinal folds extending proximally from centre of each indentation ; ornamented rims easily abraded even ; diaphragm usually transverse but sometimes

¹ In the absence of Linnaean material, type selection depends on the sole work cited by Linnaeus (1758), i.e. Ellis (1755). The woodcut figure is a good representation of part of an *Obelia* colony. It shows four internodes with three attached gonothecae but no hydrothecae. The figure is thus compatible with Linnaeus' diagnosis, which similarly does not mention hydrothecae ('Sertularia denticulis obsoletis, calycibus [= gonotheca] obovatis axillaribus, pedunculis intortis, caule dichotomo geniculato'). Some of Ellis' hydroid material was eventually incorporated in Sir Hans Sloane's herbarium which formed the basis of the biological collections of the British Museum ; but there are no specimens of *O. dichotoma* in that herbarium. Other Ellis hydroid material, some of it probably figured and hence eligible for typification, was until recently preserved in the Hunterian Museum of the Royal College of Surgeons of England (Royal College of Surgeons of England, 1830, 1860 ; Harmer, 1931). Fragments of *O. dichotoma* were evidently included (Royal College of Surgeons of England, 1860 : 137, as *Laomedea*) although it is not certain that they originated from Ellis. However, the bulk of the Ellis material was destroyed during the Second World War, and it is virtually certain that only a single specimen, of *Nemertesia* Lamouroux, 1812, survived (Dobson, 1971 ; Miss E. Allen, personal communication). The exquisite drawings listed by Harmer from which most of the plates of Ellis (1755) and Ellis and Solander (1786) were prepared still survive, however. Linnaeus gave no locality for the species, but Ellis recorded it as common on the coast of SW England.

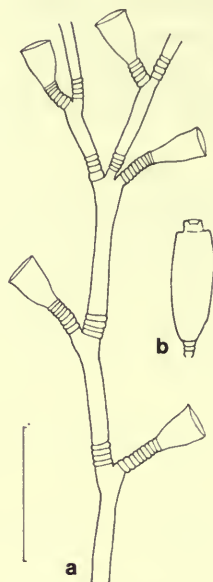


FIG. 3. *Obelia dichotoma*. (a) SW. England (1959.9.17.43). Part of hydrocaulus. (b) Ireland (1959.9.17.35). Detached gonotheca. Scale = 1000 μ m for both diagrams.

oblique. Gonothecal pedicel annulated, situated in axil of hydrothecal pedicel; gonotheca inverted cone-shaped, apex domed with central tubular aperture. Measurements – see Table 4.

TABLE 4

Measurements of the hydroid stage of *Obelia dichotoma* in μ m

	MASSACHUSETTS, U.S.A. (1915.3.6.37; Fig. 4d)	SW FRANCE (1959.11.17.4)	IRELAND (1959.9.17.35)	ISLE OF MAN, U.K. (1959.9.17.37)
HYDROTHECA				
Length (diaphragm to rim)	270–360	320–350	250–340	200–250
Breadth at rim	290–340	220–310	250–330	210–230
HYDROTHECAL PEDICELS				
Length	280–790	200–730	210–790	120–450
INTERNODES				
Length	750–1200	930–1150	830–930	430–500
Maximum breadth	080–150	070–110	120–190	080–110
Length/breadth ratio	c. 10	c. 10	c. 7	c. 4
GONOTHECA				
Length	—	750–800	870–1000	500–590
Maximum breadth	—	(obscure)	260–320	210–270

MATERIAL EXAMINED. *Atlantic Ocean* – Oban, Argyll, Scotland, 1877, several colonies in spirit, coll. A. M. Norman, 1912.12.21.276. North end of Loch Sween, Argyll, Scotland, 1 m, on *Halidrys siliquosa* (L.) Lyngbye, 1819,¹ 31 May 1962, numerous colonies in spirit and microslide, coll. W. J. Rees, 1962.6.19.13. Caol Scotnish, Loch Sween, Argyll, Scotland, 1 m, on *Halidrys siliquosa*, 30 May 1962, numerous colonies in spirit and two microslides, coll. W. J. Rees, 1962.6.19.23. Cuan Sound, Argyll, Scotland, LWST, on *Halidrys siliquosa*, 2 June 1962, numerous colonies in spirit and microslide, coll. W. J. Rees, 1962.6.19.11 (Fig. 4f). Millport, Isle of Cumbrae, Bute, Scotland, 17 September 1902, several colonies in spirit and microslide, coll. E. T. Browne, 1959.10.17.1–2. Clyde Sea, Scotland, 35 m, on stem of *Thecocarpus myriophyllum* (Linnaeus, 1758), 27 August 1920, several hydrocauli in spirit and microslide, coll. L. P. W. Renouf, 1920.9.10.1. Isle of Man,

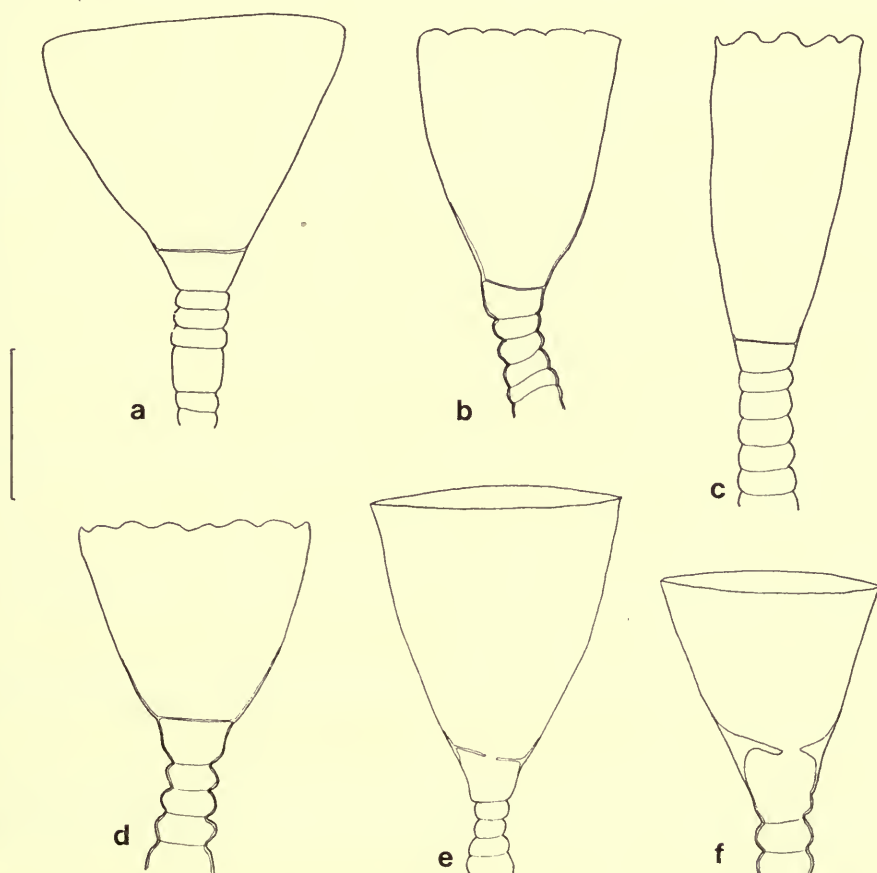


FIG. 4. *Obelia dichotoma*. Several hydrothecae showing variation in shape of rim and angle of diaphragm. (a) England (1973.7.23.1). (b) England (1929.1.1.1). (c) Probably British Isles (1920.3.1.1). (d) Massachusetts (1915.3.6.37) (Table 4). (e) Ireland (1967.6.15.106). (f) Scotland (1962.6.19.11). Scale = 250 μ m.

¹ The scientific names of algae follow Parke & Dixon (1968).

British Isles, 10 September 1894, colony on microslide, coll. E. T. Browne, 1959.9.17.47. Port Erin, Isle of Man, British Isles, 6 October 1892, colony on microslide, coll. E. T. Browne, 1959.9.17.37. Martin's Beach, Marloes Peninsula, Pembrokeshire, Wales, colony on microslide, coll. P. Dick, 1959.9.23.2. Ireland, 24 July 1902, colony on microslide, coll. E. T. Browne, 1967.6.15.106 (Fig. 4e). Ireland, 2 May 1922, five colonies on microslide, coll. E. T. Browne, 1959.9.17.35 (Fig. 3b). Plymouth, England, 14 September 1897, several colonies on piece of wood, in spirit, coll. E. T. Browne, 1954.8.3.71. Plymouth, England, 14 March 1898, colonies on two microslides, coll. E. T. Browne, 1959.9.17.32, 43 (Fig. 3a). Millbay Dock, Plymouth, England, 2 November 1906, several hydrocauli in spirit, coll. E. T. Browne, 1954.8.3.77. Mewstone Ledge, Plymouth, England, colony on microslide, coll. R. Davis, 1962.8.8.1. Tinside, Plymouth, England, intertidal, on *Fucus vesiculosus* L., 22 September 1972, several colonies in spirit and microslide, coll. P. F. S. Cornelius, 1973.7.23.1 (Fig. 4a). River Tamar, Devon, England, 0.8 km upstream of Cargreen, sublittoral, 4 October 1972, several colonies in spirit, coll. P. F. S. Cornelius, 1973.9.24.4. Weymouth Bay, Portland, Dorset, England, on test of *Asciidiella* sp. Roule (Tunicata), 20 m, several hydrocauli in spirit, coll. R. Kirkpatrick, 1897.8.9.12. Hastings, Sussex, England, several colonies in spirit, coll. & det. T. Hincks (as *Obelia flabellata*), 1899.5.1.148 (non-type). Southend Pier, Essex, England, hydrocauli in spirit, coll. R. Kirkpatrick, 1897.8.9.12. Southend Pier, Essex, England, 24 July 1927, two microslides, coll. F. J. Lambert, 1927.9.7.3. Havengore Creek, Rushey I., near Foulness I., Essex, England, microslide with three colonies, coll. F. J. Lambert, 1929.1.1.1 (Fig. 4b). 'Probably British', two colonies on microslide, 1920.3.1.1 (Fig. 4c). Banyuls, S. France, intertidal, 19 October 1959, several colonies on alga, in spirit and microslide, coll. W. J. Rees, 1959.11.17.4.

Froggy Pond, station CPI6, University of Cape Town Ecological Survey, Republic of South Africa, three fragments of colony on microslide, 1962.10.2.3 (mentioned, Millard, 1957 : 198).

Casco Bay, Maine, U.S.A., on unidentified plant, several hydrocauli in spirit and microslide, pres. Smithsonian Institution, Washington, D.C., 1880.9.27.93. Woods Hole, Massachusetts, U.S.A., on alga sp., 23 July 1911, several hydrocauli in spirit, coll. C. M. Fraser, 1915.3.6.37 (Fig. 4d).

Mediterranean/Red Seas – Suez Canal, 13 December 1924, several hydrocauli on wood in spirit and microslide, coll. Cambridge University Expedition to the Suez Canal, 1928.5.31.47, 49.

Pacific Ocean – Port Jackson, New South Wales, Australia, several colonies on algal stipe, in spirit, coll. R. von Lendenfeld, 1886.6.8.102.

No locality – Pseudo-dichotomous colony on microslide, prep. H. J. Waddington, ex A. M. Norman coll., 1919.5.26.12.

OTHER MATERIAL RECORDED. *North polar region* – Entire north coast of Russia (Linko, 1911 ; Naumov, 1969), Greenland, Bering Sea, Northern Canada and Alaska (Calder, 1970).

Atlantic – coasts of western Europe (Hincks, 1868), Mediterranean Sea and Suez Canal (Deevey, 1950), Azores (Rees & White, 1966), Ghana (Buchanan, 1957),

Tropical W. Africa (Vervoort, 1959), coast of North America from arctic to Caribbean (Fraser, 1944; Vervoort, 1967; Calder, 1970), Republic of South Africa (Millard, 1958).

Pacific – Coast of North America from arctic regions to southern U.S.A. (Fraser, 1937), Japan (Hirohito, 1969), China Sea, Galapagos Islands and coast of Ecuador (Deevey, 1950), Tasmania (Briggs, 1939, as *O. australis*), New Zealand (Ralph, 1957), Mozambique (Millard & Bouillon, 1974).

DISTRIBUTION. Widespread in the northern hemisphere, but less frequently recorded south of the equator. Most northerly record probably 77° N, 138° E, north of New Siberian Islands (Linko, 1911, as *O. longissima*); most southerly record probably 61° S, 45° E, South Orkneys (Ritchie, 1909, as *O. longissima*).

Occurs intertidally and common at depths down to 100 m, seldom below 300 m, deepest record probably 510 m (Broch, 1918; Naumov, 1969). A world distribution map was given by Deevey (1950).

REMARKS. Specimens having exceptionally thickened internodal perisarc consequently appear intermediate between this species and *O. geniculata*. Constant differences between the hydroid stages are given in Table 1.

Colonies of *O. dichotoma* showing variations in the length and nature of branching of the hydrocaulus and in the shape of the hydrothecal rim have been given specific status by some authors (see also p. 256). Alder (1857), Hincks (1868) and some subsequent authors assigned specimens with long, strongly tanned, dark main hydrocauli to *O. longissima* (Pallas, 1766), retaining only specimens with shorter, less tanned main hydrocauli in *O. dichotoma*. However, although specimens resembling *O. longissima* sensu Alder are distinctive, *Obelia* specimens in the B.M. (N.H.) collection form a continuous series between the two taxa. In addition, isolated second-order hydrocauli of 'longissima' specimens cannot be distinguished from hydrocauli of *O. dichotoma*, and the two taxa appear inseparable. Thus specimens hitherto assigned to *longissima* are probably simply older colonies of *dichotoma* s. str. Originally Pallas (1766) introduced *longissima* as an alternative, perhaps more appropriate, name for Linnaeus' species but Linnaeus (1767) gave his own name priority. Johnston (1838, 1847) also regarded *longissima* as the junior synonym. *Obelia flabellata* (Hincks, 1866) represents an intermediate point in this series and can be regarded as conspecific with *O. dichotoma*.¹

Obelia commissuralis McCrady, 1857, was founded on a medusa of which the hydroid was imperfectly known. Agassiz (1862) provided detailed descriptions of both stages and subsequent descriptions of the hydroid alone were given by Nutting (1915) and Fraser (1944). Berrill (1949), although describing the development of stolons, hydranths and medusae, did not describe systematic characters of his material. The species has been distinguished from *O. dichotoma* only once, by

¹ Certain species of medusae have been assigned to one or other hydroid species but owing to the confusion surrounding the validity of the medusa species it is probably best to regard these synonymies with caution. Thus, Sars (1835) described the medusa *Thaumantias plana* which Nutting (1915) and Stechow (1921b) referred to the hydroid *Obelia flabellata* (Hincks, 1866) (= *O. dichotoma*); Gegenbauer (1856) described the medusa *Eucope polystyla* which Mayer (1910) provisionally referred to *O. longissima* hydroid (= *O. dichotoma*); and Agassiz (1865) described the medusa *Eucope fusiformis* which Bedot (1910) synonymized under *O. fusiformis* (= *O. dichotoma*).

Nutting (1915) in a key to the genus, on the basis of the number of annuli per internode and the arrangement of the side-branches. These characters are variable in *O. dichotoma* and on present evidence *O. commissuralis* appears invalid.

The original description of *O. australis* von Lendenfeld, 1885a, is inadequate for identification, but the subsequent restriction by Bale (1888) is clearly referable to *O. dichotoma*, as also is the non-type material identified as *O. australis* by von Lendenfeld (1886.6.8.102). Recently the species was distinguished by Ralph (1957) solely on the presence of an oblique hydrothecal diaphragm, a character noted by Bale and present in von Lendenfeld's material. However, this is a common variation in specimens of *O. dichotoma* from British localities (Fig. 4e-f) and its occurrence in southern populations cannot be considered grounds for maintaining *O. australis* distinct.

Schizocladium ramosum Allman, 1871, was referred to *Obelia* sp. by Billard (1901a, 1904a) and to *O. geniculata* by Bedot (1918, 1925). However, Allman originally likened the species to *O. dichotoma* and his illustration, showing a much-branched campanularian hydroid with unthickened internodal perisarc, has greater resemblance to *O. dichotoma* to which the species is here referred.

Following Millard (1966: 483) *Campanularia obtusidens* Jaderholm, 1905a, is assigned to *O. dichotoma*. Bedot (1925: 302) had previously placed it in *O. dubia* Nutting, 1901, which Millard also assigned to *O. dichotoma*. The original description did not mention gonothecae, and those described by Fraser (1944) differed from those of *O. dichotoma* only in being stolonial. It seems probable that Fraser's material was simply a growth-form of *O. dichotoma*.

Campanularia obtusidentata is a name ascribed to Vanhoffen (1910: 272) by Bedot (1925: 302) in the latter's synonymy of *O. dubia* Nutting. However, the name does not occur in Vanhoffen's paper and seems to have been used by Bedot alone. It is clearly a *lapsus* for *obtusidens*.

MEDUSAE. Those reared from both this species and from *O. geniculata* have been found to resemble *O. lucifera* (Forbes, 1848) (summary in Russell, 1953). Their relation with the hydroid is discussed below (p. 278). They were first recorded by Baster (1762) who saw their release on 3 June 1757. The subsequent history of the elucidation of the life-cycle was reviewed by van Beneden (1844) and briefly by Hincks (1868).

***Obelia geniculata* (Linnaeus, 1758)**

(Figs 1, 5)

Sertularia geniculata Linnaeus, 1758: 812; Pallas, 1766: 117-119; Linnaeus, 1767: 1312 (= *S. flexuosa* Linnaeus); Maratti, 1776: 34.

Laomedea lairii Lamouroux, 1816: 207; Lamouroux, 1821: 14, pl. 67, fig. 3.

Campanularia geniculata: Meyen, 1834: 195-196, pl. 31, figs 3-5; Bedot, 1905: 51-52 (= *C. prolifera* Meyen; *C. cavolinii* Deshayes & Edwards¹; *C. caulini* Chiaje¹).

Campanularia prolifera Meyen, 1834: 198-201, pl. 33, figs 1-5.

Sertularia prolifera: Deshayes & Edwards, 1836: 139.

Laomedea geniculata: Johnston, 1838: 151-152, pl. 21, figs 1-2; Johnston, 1847: 103-104, pl. 25, figs 1-2; Gosse, 1853: 84-90, pl. 4; Vervoort, 1946a: 294-298, figs 129-131 (= *L.*

¹ *C. cavolinii* and *C. caulini* are here assigned to *O. dichotoma*.

- lairii* Lamouroux; *Sertularia prolifera*: Deshayes & Edwards; *Campanularia cavolinii* Deshayes & Edwards¹; *Schizocladium ramosum* Allman¹).
- Eucope diaphana* L. Agassiz, 1862: 322-325, pl. 34, figs 1-9; (non A. Agassiz, 1865: 83-85, figs 115-125; indeterminate).
- Obelia geniculata*: Allman, 1864: 372; Hincks, 1868: 149-151, pl. 25, fig. 1, 1a (= *Eucope diaphana* L. Agassiz; *E. alternata* A. Agassiz); Bedot, 1910: 338-340 (= *Laomedea lairii* Lamouroux; *Schizocladium ramosum* Allman¹; *O. gymnophthalma* Spagnolini); Mayer, 1910: 249-252, figs 132-133 (= *E. diaphana* L. Agassiz; *E. alternata* A. Agassiz; ? *E. polygena* A. Agassiz; *E. fusiformis* A. Agassiz); Vanhoffen, 1910: 304-306, fig. 25 (= *Monosklara pusilla* von Lendenfeld); Bedot, 1916: 162-164 (= *E. diaphana* L. Agassiz); Bedot, 1925: 304-307 (= *E. polygena* A. Agassiz); Vannucci Mendes, 1946: 551-552, pl. 2, figs 14-15; Russell, 1953: 302, fig. 185a; Naumov, 1960: 261-263, figs 147-148; Naumov, 1969: 282-283, figs 147-148.
- Eucope alternata* A. Agassiz, 1865: 86 (nom. nov. pro *E. diaphana* L. Agassiz, non *Thaumantias diaphana* A. Agassiz).
- Eucope polygena* A. Agassiz, 1865: 86-87, fig. 126; Bedot, 1912: 332.
- Eucope fusiformis* A. Agassiz, 1865: 90, figs 132-133.
- Obelia gymnophthalma* Spagnolini, 1871: 186 [nom. nov. pro medusa stage of *O. geniculata* (Linnaeus)].
- Monosklara pusilla* von Lendenfeld, 1885b: 911-912, pl. 40, figs 1-3.
- Obelia geniculata* var. I Marktanner-Turneretscher, 1890: 207-208.
- Obelia geniculata* var. II Marktanner-Turneretscher, 1890: 208.
- Obelia geniculata* var. III Marktanner-Turneretscher, 1890: 208.
- Campanularia coruscans* Schneider, 1897: 482; [syn. nov.].
- Obelia geniculata* f. *subsessilis* Jaderholm, 1905a: 2, pl. 1, fig. 2.
- Obelia geniculata* f. *gaussi* Vanhoffen, 1910: 305, fig. 25d.
- Obelia geniculata* f. *subtropica* Ralph, 1956: 285.
- Obelia geniculata* f. *intermedia* Ralph, 1956: 285.
- Obelia geniculata* f. *subantarctica* Ralph, 1956: 285.

TYPE SPECIMEN AND TYPE LOCALITY. Ellis, 1755: 22, pl. 12, fig. B, but not fig. b²; Dover, Kent, England; intertidal, on fucoid alga. Present location of specimen unknown.

¹ *C. cavolinii*, and *S. ramosum* are here assigned to *O. dichotoma*.

² Linnaeus (1758) gave no type locality and cited only Ellis' description and figure. The illustration shows a specimen having typical *Obelia* gonothecae but lacking hydrothecae. Linnaeus' designation 'Sertularia denticulis obsoletis, calycibus [= gonotheca] obovatis subrostratis, caule geniculato flexuoso simplici' similarly describes the gonotheca, but omits reference to the hydrotheca. It is likely that the specimens in the Linnean herbarium of the Linnean Society of London (Savage, 1945) were not before Linnaeus when he wrote his designation since they possess both hydrothecae and gonothecae (see footnote, p. 267). It seems probable, therefore, that Linnaeus based his designation solely on Ellis' figure. The locality from which the figured specimen was obtained was not given precisely, although Ellis stated: 'This coralline was found at Dover; and I have lately received some specimens from Harwich; so that I believe it is not uncommon on our coasts.' The figured specimen is perhaps more likely to have come from the earlier locality, Dover, as the Harwich material possibly came to Ellis too late for an illustration to be prepared. He recorded it on 'podded *Fucus*', which could refer either to *Fucus vesiculosus* or *Ascophyllum nodosum* (L.) Le Jol (J. M. Price, personal communication).

As with *O. dichotoma*, it is virtually certain that the figured specimen no longer survives (see footnote, p. 267). However, it remains possible that some other hydroid specimens in the Linnean herbarium are Ellis' figured material and hence type, since as late as 1 January, 1767, Linnaeus had received hydroid material from no source but Ellis (Smith, 1821: 196). The type-series of *Sertularia echinata* Linnaeus, 1761, to be described in a later paper (Cornelius, 1975: *in press*), indicates that it at least had reached Linnaeus by or during 1761. This is evident since the original designation of *S. echinata* includes characters of both species represented in the type-series, which was mixed. Thus Harmer (1930: 84) was apparently wrong in suggesting that Linnaeus received his first batch of Ellis' hydroid material at the end of 1766. Unfortunately the correspondence between Linnaeus and Ellis during 1763 and 1764 is missing (Smith, 1821: 164 (footnote); Ahrling, 1885: 55, 77; Savage, 1948: 23-25; T. O'Grady, personal communication) so it is not at present clear which if any specimens were sent to Linnaeus during those two years.

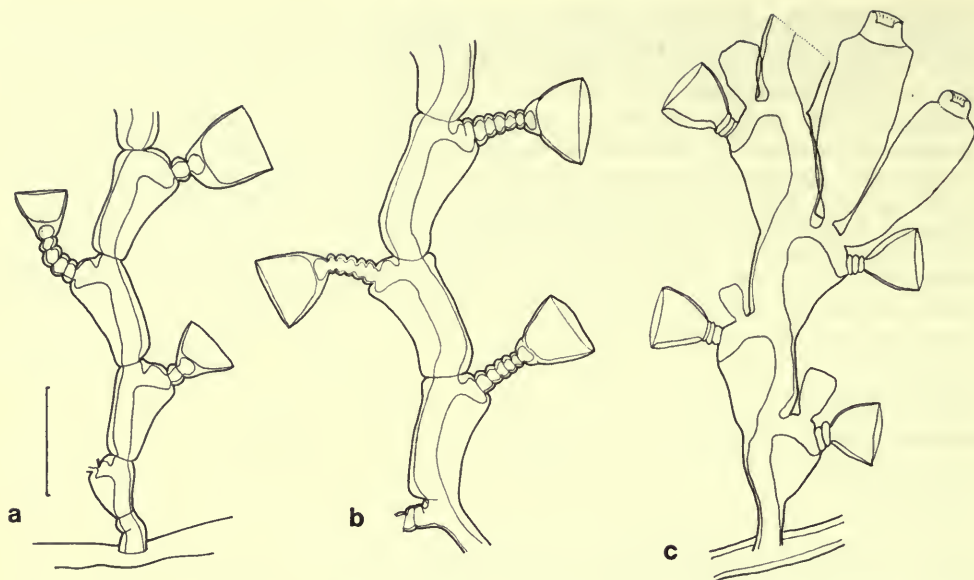


FIG. 5. *Obelia geniculata*. Parts of three hydrocauli to show differing extents of inter-nodal thickening. (a) Republic of South Africa (1964.8.7.80). (b) SW. England (1966.10.28.7). (c) Republic of South Africa (1936.2.4.13), probably the extreme of shortening and thickening. Scale = 500 μ m throughout.

DIAGNOSIS OF SPECIES. *Obelia* hydroid usually with unbranched, erect, flexuose, monosiphonic hydrocauli; internodes short, curved, with prominent internal thickening of perisarc below origin of pedicel; hydrotheca even-rimmed.

DESCRIPTION. Colony comprises attached stolons from which arise vertical monosiphonic hydrocauli, usually unbranched, up to 40 mm (Fig. 5). Hydrocaulus flexuose; internodes short, curved, internally thickened below origin of each pedicel, usually with one to five proximal annulations. Pedicel variable in length, attached to short lateral process near distal end of internode, annulated throughout or with smooth central portion. Hydrotheca broad, even-rimmed, bell-shaped, length about equal to width at rim. Gonotheca situated on short annulated pedicel in axil of hydrotheca; conical, wider distally, apex domed with narrow tubular aperture. Measurements – see Table 5.

MATERIAL EXAMINED. *Atlantic Ocean* – No locality (? Baltic), probably after 1758, coll. Linnaeus, two herbarium sheets, Linnean Society of London cat. no. 1298.19–20 (Savage, 1945).¹ Balta Sound, Shetland, on *Laminaria* sp., 1867,

¹ Sheet 1298.19 bears a specimen of a fucoid alga with an attached colony of *O. geniculata* comprising about 20 erect hydrocauli. All the hydrothecae are missing, and only two gonothecae remain. Sheet 1298.20 bears four specimens, one at the top of the sheet, two side by side in the centre and one at the bottom. The top specimen is a piece of *Laminaria* sp. Lamour. to which a colony of *O. geniculata* is attached. It has many hydrothecae but no gonothecae. Of the two centre specimens that on the left is a piece of alga with no hydroids attached, and that on the right is another piece of alga, probably *Fucus* sp. L. or *Laminaria* sp. with colonies of *O. geniculata* attached. A few hydrothecae are present, but no gonothecae. The specimen at the bottom of the sheet is not *Obelia*, and is not readily identified as it is decayed. It appears from an attached label to have been added later. These specimens are probably not type material (see footnote, p. 273).

TABLE 5

Measurements of the hydroid stage of *Obelia geniculata* in μm

	SW ENGLAND (1973.9.26.1)	REPUBLIC OF SOUTH AFRICA (1936.2.4.13 ; Fig. 5c)*	W SCOTLAND (1962.6.19.5)†
HYDROTHECA			
Length (diaphragm to rim)	240–290	220–270	210–300
Breadth at rim	270–390	250–310	230–320
Maximum thickness of hydrothecal perisarc	20	50	20
HYDROTHECAL PEDICELS			
Length	070–170	070–140	240–370
INTERNODES			
Length	600–700	470–590	600–820
Maximum breadth	160–250	290–440	210–270
Length/breadth ratio	c. 3	c. 1–1.5	c. 3
Maximum diameter of asymmetric thickening	050–100	270	100
GONOTHECA			
Length	700–800	820–940	1030–1070
Maximum breadth	240–300	290–340	270–320
GONOTHECAL PEDICELS			
Length	030–080	020–030	090–100

* Specimen resembles *O. geniculata* 'var. *subsessilis*' Jaderholm.

† Specimen has long internodes in distal parts.

several colonies in spirit and microslide, coll. A. M. Norman, 1912.12.21.262. Clachan Bridge, Seil, Argyll, Scotland, 1 June 1962, two hydrocladia on microslide, coll. W. J. Rees, 1962.6.19.5. Creagan Narrows, Argyll, Scotland, MLWST, on *Fucus vesiculosus*, 10 September 1970, several hydrocladia, spirit, coll. P. F. S. Cornelius, 1971.5.11.18. Port Erin, Isle of Man, British Isles, 26 September 1892, two hydrocauli on microslide, coll. E. T. Browne, 1959.9.17.29. Port St Mary, Isle of Man, British Isles, on *Laminaria* sp., 30 m, several hydrocladia in spirit, coll. J. Lomas, 1886.1.9.2. St Ives, Cornwall, England, hydrocaulus on microslide, coll. R. E. W. Vallentin, 1935.8.12.24. Looe, Cornwall, England, LWM, on *Cystoseira* sp. Agardh, 21 September 1972, several hydrocauli in spirit, coll. P. F. S. Cornelius, 1973.9.24.2 (Fig. 1). Looe, Cornwall, England, LWM, on *Laminaria saccharina* (L.) Lamour., 21 September 1972, several hydrocauli, coll. P. F. S. Cornelius, 1973.9.24.3. Drake's Island, Plymouth, Devon, England, June 1965, three hydrocauli on microslide, coll. R. C. Vernon, 1969.12.1.20. Torpoint pontoon, Plymouth, Devon, England, 13 August 1963, four hydrocauli on microslide, coll. R. C. Vernon, 1973.9.26.1. Plymouth, Devon, England, 29 September 1947, coll. E. White, two hydrocauli on microslide, 1947.10.8.1. Plymouth, Devon, England, 29 August 1947, coll. E. White, hydrocaulus on microslide, 1947.10.8.3. R. Yealm, Devon, England, MLWST, on *Fucus serratus* L., 4 July 1973, several

colonies in spirit and six microslides, coll. P. F. S. Cornelius, 1973.7.23.2. R. Yealm, Devon, England, MLWST, on *Laminaria* sp., 4 July 1973, several colonies in spirit and six microslides, coll. P. F. S. Cornelius, 1973.7.23.3. Start Bay, Devon, England, on *Laminaria* sp., 10 m, spirit material and microslide, coll. R. Kirkpatrick, 1893.8.7.7. Eddystone grounds, western English Channel, 2 September 1898, several hydrocauli on microslide, coll. E. T. Browne, 1959.9.17.30. Great Britain Rock, St Mary's, Scilly Isles, on *Laminaria* sp., 10 m, 22 July 1964, several colonies in spirit and two microslides, coll. Queen Mary College expedition, 1966.10.28.2. Great Britain Rock, St Mary's, Scilly Isles, 15 m, 23 July 1964, three hydrocauli on microslide, coll. Queen Mary College expedition, 1966.10.28.7 (Fig. 5b).

South of Fugloy, Espegrend, Norway, 40 m, on bryozoan, 7 August 1962, spirit material and microslide, coll. W. J. Rees, 1962.11.7.47.

Nez de Joburg, NW. of Cherbourg Peninsula, France, on *Laminaria* sp., 3 May 1965, several colonies in spirit, coll. A. M. Clark, det. W. J. Rees, 1965.5.14.2.

Newport, Rhode Island, U.S.A., on wood, 25 m, several colonies in spirit and microslide, pres. Smithsonian Institution, 1890.8.23.14. Potts Point, South Harspowell, Maine, U.S.A., on *Fucus* sp., seven hydrocauli on microslide, coll. C. M. Fraser, 1915.3.6.38. Vineyard Sound, Massachusetts, U.S.A., on *Laminaria* sp. spirit material and microslide, pres. Smithsonian Institution, 1880.9.27.94.

Gough Island, Tristan da Cunha, 22 April 1904, hydrocaulus on microslide, coll. Scottish National Antarctic Expedition, det. J. Ritchie, 1964.8.7.79.

Oudekraal, Republic of South Africa, two microslides, University of Cape Town Ecological Survey, 1936.2.4.13 (Fig. 5c). Entrance to Saldanha Bay, Cape Colony, Republic of South Africa, 50 m, 21 May 1904, two hydrocauli on microslide, coll. Scottish National Antarctic Expedition, det. J. Ritchie, 1964.8.7.80 (Fig. 5a).

Pacific Ocean – New Zealand, 20 hydrocauli on algal thallus in spirit, coll. R. von Lendenfeld, 1886.6.8.107, ('*Monosklera pusilla*', det. von Lendenfeld, not type). Off Port Ross, Auckland Islands, New Zealand, on *Laminaria* sp., 28 March 1904, several colonies in spirit, coll. 'Discovery' Antarctic Expedition, 1907.8.20.44.

OTHER MATERIAL RECORDED. *North Atlantic* – White Sea (Linko, 1911), Jan Mayen Island, Iceland, coast of Norway at least to 68° N (Broch, 1918); Barents Sea, European coast and Mediterranean Sea (Naumov, 1969); fjords of West Greenland (Calder, 1970); whole Atlantic coast of North America (Fraser, 1944); Coats Island, Hudson Bay (63° N) (Calder, 1970); parts of Caribbean (Vervoort, 1968).

South Atlantic – Zaire (Leloup, 1939), Ghana (Buchanan, 1957), Luderitz Bay (26° S) and other localities in Republic of South Africa (Broch, 1914; Millard, 1957, 1966); Kerguelen Island (Vanhoffen, 1910); Falkland Islands (M. W. Robins, personal communication); South Georgia (Deevey, 1950) and Brazil (Vannucci Mendes, 1946).

North Pacific – Japan (Yamada, 1958); British Columbia and whole of U.S.A. coast except Alaska (Fraser, 1937).

South Pacific – Chile (Jaderholm, 1905b), Indonesia and Galapagos Islands (Deevey, 1950), West Australia, South Australian Bight, Victoria, New South

Wales and Tasmania (Hodgson, 1950), Macquarie Island (Briggs, 1939), New Zealand, adjacent seas between 35° S and 49° S and the Chatham Isles (Ralph, 1956, 1961).

Indian Ocean – Two localities in southern India (Mammen, 1965), Mozambique (Millard & Bouillon, 1974).

DISTRIBUTION. Almost cosmopolitan in continental shelf seas. Deevey (1950) stated that *O. geniculata* is the most widely distributed of all hydroids, being absent only from the northern Indian Ocean and the tropical West Atlantic (although subsequently recorded from the Caribbean). Apart from South Georgia and Macquarie Island there appear to be no records also from the Southern Ocean, and the species appears unrecorded from much of the Pacific, including northern parts of the Australian mainland, Brisbane and the Great Barrier Reef (Ralph, 1956).

In the northern hemisphere the species extends almost as far north as *O. dichotoma*, being known from the White Sea. Although it was reported absent from Greenland by Broch (1918) and was not found by Kramp (1932) in some west Greenland collections, Calder (1970) nevertheless recorded the species from both east and west Greenland, but did not cite material.

REMARKS. Variation in the hydroid stage of this species occurs mainly in the angle of flexure between internodes, the asymmetric thickening of the internodal perisarc, the length to breadth ratio of the internodes and the shape of the hydrotheca. Apart from the form of the hydrotheca, these characters can be placed in a series ranging from specimens with shallow angles between internodes, little internodal thickening and proportionately long internodes to more flexuous specimens with greater internodal thickening and shorter internodes (Fig. 4a–c).

The occurrence of these variations has prompted authors to recognize several varieties and formae. Vanhoffen (1910), however, was of the opinion that the following of these taxa fall within the limits of normal variation: Varieties *I*, *II* and *III* of Marktanner-Turneretscher, 1890; forma *gaussi* Vanhoffen, 1910 (nom. nov. pro var. *I* of Marktanner-Turneretscher) and forma *subsessilis* Jaderholm, 1905b. Further varieties (*subtropica*, *intermedia* and *subantarctica*) were described by Ralph (1956) based on variations in length of hydrocaulus, number of annulations of the internodes, amount of branching and linear dimensions of all structures. These characters are known to be variable (p. 256) and it is perhaps best at present not to regard them as systematically valid.

The species appears to be variable within the above limits over the whole of its range. Thus, specimens showing the extreme of shortening and internodal thickening have been reported from Chile, Kerguelen Island and the Republic of South Africa (Jaderholm, 1905b; Vanhoffen, 1910; Fig. 5c), while specimens with both minimal and maximal thickening are known from the English Channel (1959.9.17.30). Almost the full range of variation is represented in British specimens in the BM(NH) collection, and the naming of distinct varieties seems unnecessary.

Hammett & Hammett (1945) followed the seasonal morphological changes in colonies of *O. geniculata* during several summers in Massachusetts but variations in features of accepted systematic importance were not reported. More recently detailed accounts of variation in New Zealand populations by Ralph (1956) and Ralph & Thomson (1968) demonstrated that over a wide geographical range and

from season to season at a single locality certain morphological characters varied with temperature. Low temperatures induced longer colonies with longer internodes, and colonies from warmer localities showed a reduction in branching.

Laomedea lairii Lamouroux, 1816, was placed in the present species by Bedot (1901) and also by Billard (1909) who examined the type specimen. The specimen was subsequently destroyed in the Second World War (Redier, 1967).

Campanularia coruscans Schneider, 1897, was originally stated to release a medusa and was subsequently assigned to *Obelia* by Stechow (1921b, 1923b). The wide distal shelf in each internode supporting the hydrotheca, as described by Schneider, suggests that *C. coruscans* is referable to *O. geniculata*.

MEDUSAE. Those reared from both this species and *O. dichotoma* have been found to resemble *O. lucifera* (Forbes, 1848) (summary in Russell, 1953). Their relation with the hydroid is discussed below. The earliest record of medusa release in *O. geniculata* seems to be that of F. W. L. Thomas (*in* Johnston, 1847: 467), who commented on the similarity between the medusa of this species and that of *O. dichotoma*. Medusae of *O. geniculata* were apparently first illustrated by Gosse (1853).

THE MEDUSA PROBLEM

Many nominal species of *Obelia* are based solely on the medusa stage, most having been described in the past 100 years (references in Mayer, 1910; Bedot, 1901-25; Kramp, 1961). However, they are very similar and it is likely that many are conspecific (Kramp, 1961). As noted by Russell (1953), it is at present impossible to relate them to the hydroid species, and it may remain so until further rearing work has been done and the characters of the medusae reassessed.

Although all three species recognized from the hydroid stage occur in British seas, only two nominal species of medusae are known. The five taxa recorded are as follows (modified from Russell, 1953):

HYDROIDS

<i>O. bidentata</i>	Mature medusa not described
<i>O. dichotoma</i>	Mature medusa resembles <i>O. lucifera</i>
<i>O. geniculata</i>	Mature medusa resembles <i>O. lucifera</i>

MEDUSAE

<i>O. lucifera</i>	Reared to maturity from both <i>O. dichotoma</i> and <i>O. geniculata</i> , and known from the plankton
<i>O. nigra</i> Browne, 1900	Known only from the plankton

It has been suggested by elimination (Browne, *in* Kramp, 1927; Russell, 1953) that *O. longissima* might prove to be the hydroid of *O. nigra*. However, this cannot be the whole answer if, as is shown above, *O. longissima* is conspecific with *O. dichotoma* from which *O. lucifera* has been reared. The occurrence of the hydroid *O. bidentata* in the North Sea and English Channel, and the fact that the appearance of its medusa when adult is unrecorded, add further complications.

The possibility that *O. nigra* alone is released from *O. bidentata* is unlikely as the two species have different distributions in western Europe. Thus, the hydroid occurs no further north than the coasts of France, Belgium and Holland and the southern North Sea (Vervoort, 1946a; Leloup, 1952; Hamond, 1957; Kramp, 1961; Teissier, 1965), while the medusa is known from as far north as western Scotland, Iceland and Bergen, Norway (Browne, 1905; Thiel, 1932; Kramp, 1939; Rees, 1953).

Sir Frederick Russell (personal communication) is of the opinion that in the seas around the British Isles *O. nigra* is associated with mixed oceanic and coastal water typified by the presence of *Sagitta elegans* (Chaetognatha), while *O. lucifera* occurs in coastal water of which *S. setosa* is characteristic (Meek, 1928). *O. nigra* is said to be larger than *O. lucifera* and to have darker pigmentation around the tentacle bases (Russell, 1953). It has long been suspected that the mixed water is more productive than British coastal water (Russell, 1939), and as suggested by Browne (in Kramp, 1927) the larger size characteristic of *O. nigra* might simply reflect better feeding opportunities. Thus it is possible that medusae from all three hydroid species develop *O. lucifera* characters in coastal water and those of *O. nigra* in more productive areas. It is noteworthy that although Browne recorded both species of medusae off Plymouth between 1897 and 1899, published records suggest that he never obtained them together (Marine Biological Association, 1957). This perhaps indicates that the furthest extent of mixed water into the English Channel then varied in position around Plymouth. Although mixed oceanic and coastal water frequently reached Plymouth in the 1920's, it did not do so for some decades after the early 1930's (Russell *et al.*, 1971). During that time *O. lucifera* was the prevalent species (Russell, personal communication), further suggesting a correlation with water mass and, possibly, feeding opportunity.

Although it might be inferred from the available evidence that the two medusa species are conspecific, the possibility that they are genetically distinct nevertheless remains open, while another possibility is that the hydroid of *O. nigra* is as yet undescribed.

SPECIES TRANSFERRED TO OTHER GENERA

Although *Campanularia gelatinosa* (Pallas, 1766) was reported to release a medusa by van Beneden (1844), his illustrations identify his material as *Obelia dichotoma*. Hincks (1868) was aware of this misidentification, but independently described a medusa stage in *C. gelatinosa* and placed the species in *Obelia*. Later Maitland (1876: 13) identified the medusa *Obelia marina* (Slabber, 1769) with *Campanularia gelatinosa* auct. (? sensu Hincks). A medusa has not been reported since in the species, and recent opinion (Vervoort, 1946a; Naumov, 1969; J. Clare, personal communication) is that one is not released. It is possible that Hincks mistook the large ova characteristic of *C. gelatinosa* for developing medusae.

Campanularia denticulata Clarke (1876: 9, pl. i, fig. 4) has usually been referred to *Obelia* (references in Bedot, 1912-25) although Pictet (1893) assigned it to *Clytia noliiformis* McCrady, 1857. Mammen (1965) did not agree with Pictet's synonymy

and Clarke's nominal species still stands as *Campanularia denticulata*. However, the acutely cusped hydrothecal rim originally described suggests that the species should nevertheless be referred to *Clytia*.

Obelia marginata Allman (1877 : 9-10, pl. 6, figs 1-2) is now accepted as a species of *Cnidoscypus* Splettstösser, 1929 (Vervoort, 1968).

The two nominal species *Obelia longicyatha* Allman, 1877, and *O. longicyatha* Thornely, 1899, are discussed above under *O. bidentata* (p. 264).

Eucope annulata von Lendenfeld (1885a : 602-603, pl. 28, figs 53-57) was placed in *Obelia* by Bedot (1925 : 298), but von Lendenfeld's illustration shows an approximately hemispherical medusa quite unlike *Obelia* and Kramp (1961) referred the species to *Phialella* Browne, 1902.

Campanularia serrulata Bale (1888 : 757, pl. 12, fig. 4) was referred to *Obelia* by Thornely (1899) and Mayer (1910, mis-spelt as *O. serratula*) but later transferred to *Clytia* by Bedot (1918, 1925). Although the triangular cusps on the hydrothecal rim shown by both Bale and Mayer are typical of *Clytia*, the gonotheca described by Thornely was unlike that of *Clytia* in having a rounded, truncate top. However, as the gonotheca may have been immature, it is still possible that the three authors were describing the same species. Nutting (1927), however, provided the new name *Obelia thornelyi* for Thornely's material. Nevertheless, the nature of the hydrothecal rim described by both Bale and Mayer suggests that their material at least should be referred to *Clytia*.

Campanularia castellata Clarke (1894 : 71-72) (= *Obelia castellata* Clarke, 1894 : 73, pl. 1, fig. 3-8, pl. 2, fig. 9) is referable to *Campanularia gelatinosa* (Pallas, 1766) as it had a castellated hydrothecal rim. Bedot (1918 : 196 ; 1925 : 300) mis-spelt the name as *castellana*.

Campanularia kincaidi Nutting (1899 : 743-744, pl. 62, figs 2a-c) was referred to *Laomedea* by Leloup (1940 : 21) and to *Obelia* by Rees & White (1966 : 277). Its creeping habit and singly cusped hydrothecal rim are reminiscent more of *Clytia*, however ; and in the absence of information on the life-history the species is probably best excluded from *Obelia*.

Obelia linearis Thornely (1899 : 453, pl. 44, fig. 6), although retained in *Obelia* by Mayer (1910 : 257), was transferred to *Clytia* sp. by Mammen (1965 : 21). The presence of a deeply cleft hydrothecal rim and a reflexed gonothecal aperture support Mammen's opinion.

Obelia delicatula Thornely (1899 : 453, pl. 44, fig. 7) was assigned to *Clytia* by Stechow (1923b) and Blackburn (1942). Although the medusa is unknown, its stolonal gonotheca and sharply-cusped hydrothecal rim are features typical of *Clytia* and the species is for the present probably best assigned to that genus.

Obelia austrogeorgiae Jaderholm (1904b : 7 ; 1905b : 17, pl. 17, figs 1-2) has not been shown to produce a medusa and is here provisionally referred to the genus *Campanularia*. The species has also been recorded by Nutting (1915) and Vervoort (1972b, as *Laomedea* (*Obelia*) *austrogeorgiae*). As reported by Jaderholm, gonothecae are absent from the schizoholotype material (1960.8.29.34) which was examined during the present work, and have not yet been recorded for the species. At present, therefore, its generic affinity is obscure, but the bimucronate hydrothecal rim

originally described suggests that Mayer (1910) may have been correct in assigning the species to *O. bidentata*.

Obelia striata Clarke (1907: 9-10, pls 6-7) is a distinctive hydroid known since the first description to release a medusa with four tentacles. It was, therefore, referred to *Clytia* sp. by Rees & Thursfield (1965) and to *Clytia gravieri* (Billard, 1904b) by Millard & Bouillon (1973), while Vervoort (1966) assigned it to *Laomedea* (*Phialidium*). As adult medusae are unrecorded it is difficult to assign the species to a particular genus with confidence, but the four tentacles of the young medusa suggest that it is not an *Obelia* species. Vervoort (1968: 19) considered that *Laomedea tottoni* Leloup, 1935, was very similar to *O. striata* Clarke.

Laomedea (*Obelia*) *bistriata* Leloup (1931: 4-6, figs 8-11) was referred to *Clytia hendersonae* Torrey, 1904, by Mammen (1965) and to *C. gravieri* (Billard, 1904b) by Vervoort (1967), Schmidt (1972) and Millard & Bouillon (1973). The spines associated with the cusps on the hydrothecal rim were illustrated by Leloup (1931, 1932) and Vervoort, and resemble closely those of *O. bidentata*. Although such spines are otherwise unreported from *Clytia*, Vervoort's observation that the developing medusa has a 'strongly convex umbrella', and Millard & Bouillon's that it has four tentacles, are evidence that the species should be assigned to the genus *Clytia*.

As stated in the generic diagnosis, several of the species admitted to the genus *Obelia* by Naumov (1960, 1969) are here referred to the genera *Campanularia* and *Gonothyrea*. The species involved are *Campanularia gelatinosa* (Pallas, 1766), *C. gracilis*¹ Sars, 1850 (non *O. gracilis* Calkins, 1899, = *O. dichotoma*), *C. flexuosa* (Hincks, in Alder, 1856) and *G. loveni* (Allman, 1859), none of which releases a medusa.

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¹ Vervoort (1946a: 285) had previously suggested that the correct name for Sars' species is *C. pelagica* van Breemen, 1905.

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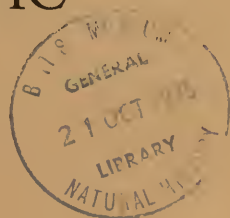
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By H. S. J. ROE

SYNOPSIS

One new genus, nine new species, and nineteen undescribed males of known species of calanoid copepods are described. A further eighteen rare or poorly known species are described or commented upon. Five existing species are transferred to the new genus; new synonymies are proposed for six species, and two species are recorded as *incertae sedis*. All the specimens were taken from vertical series of closing net hauls made in the northeastern Atlantic.

INTRODUCTION

For some years the Institute of Oceanographic Sciences has been investigating the vertical distributions and migrations of zooplankton and nekton in the northeastern Atlantic. These investigations have been based largely upon a series of vertical hauls made with horizontally towed opening and closing net systems. The calanoid copepods have now been analysed from two of these series. The results of the first, the RRS 'Discovery' SOND cruise in 1965, have been given previously (Roe, 1972a, b, c, d). The SOND series was taken with a modified Indian Ocean Standard Net (the N113H), fitted with a catch dividing bucket, in a position off Fuerteventura in the Canary Islands. Details of the sampling methods used in this series are given by Foxton (1969), Angel (1969) and Roe (1972a).

The second series was made in 1969 in a position centred on 18°N 25°W near the Cape Verde Islands. A day and a night series of hauls was made with an acoustically controlled net system. This comprises two rectangular midwater trawls, one of 8 m² mouth area and mesh of 4.5 mm (RMT 8), the other of 1 m² mouth area and mesh 0.32 mm (RMT 1), combined within the same frame. This net system, designated the RMT 1+8, is described by Baker, Clarke & Harris (1973). The series was taken at 1250–0 m depth and was fished in the manner described by Baker *et al.*

Both these series contained a number of very rare calanoid copepods, several undescribed sexes of known species and some new species. These specimens are all described below. The geographical positions given for each species are approximate; more accurate positions are listed at the Institute of Oceanographic Sciences.

TAXONOMY

Family SPINOCALANIDAE

The RMT 1 collections contain females of the following species of *Spinocalanus*: *S. abyssalis* Giesbrecht, 1888; *S. magnus* Wolfenden, 1904; *S. spinosus* Farran, 1908; *S. horridus* Wolfenden, 1911; *S. angusticeps* Sars, 1920; *S. brevicaudatus*

Brodsky, 1950; *S. parabyssalis* Park, 1970; *S. hoplites* Park, 1970; *S. usitatus* Park, 1970; *S. pteronus* Park, 1970. These females all agree with previous descriptions and all except *S. angusticeps* fit Park's (1970) partial key to the genus. Together with these females were the males of five species. Three of these are more or less tentatively identified as *S. abyssalis*, *S. brevicaudatus* and *S. sp.* Grice & Hulsemann, 1967, but the remaining two could not be attributed to any known species. Since the males of many species of *Spinocalanus* are unknown and as the present specimens are all incomplete they are not considered here to be new species.

Spinocalanus ? *abyssalis* Giesbrecht, 1888

MATERIAL EXAMINED: 56 males from 13 RMT 1 hauls made at 1020–300 m depth in a position 18°N 25°W, between 12 and 16 November 1969. 44 specimens deposited at the British Museum (Natural History), reg. no. 1974:462–482.

DESCRIPTION. Male (Fig. 1a–j): Body length 1.06–1.22 mm with a mean of 1.14 mm (35 specimens). The cephalothorax is stout and 1.7 times as long as the 5-segmented abdomen. In lateral view the cephalothorax is arched dorsally. The head and 1st thoracic segment are completely fused and thoracic segments 4 and 5 are partially so. The 3rd thoracic segment has protruding corners in dorsal view. There is no rostrum. The anal segment is very short and telescoped into the 4th abdominal segment. The 1st antenna has 19 free segments and reaches to about halfway along the 2nd abdominal segment; the basal eight segments have large flattened sensory filaments; the 1st segment has a small group of spines. The remaining mouthparts and legs are as shown. A satisfactory preparation of the 1st maxilla was not obtained but it appears to be similar to that of *S. ? brevicaudatus* (p. 300). The 2nd maxilla and maxilliped are weakly chitinized and have small feeble setae. The swimming legs of all specimens are damaged. The 5th pair of legs reaches back to the hind edge of the 2nd abdominal segment; the right endopod and the terminal spine of the left exopodite are broken off in all the dissected specimens.

REMARKS. Brodsky (1950) and Park (1970) discussed the synonymy of this species. The present males do not fit the description of any known *Spinocalanus* male. They were taken at depths where the most abundant spinocalanids were females of *S. abyssalis* (2022 specimens), *S. spinosus* (336), *S. magnus* (111), *S. brevicaudatus* (73) and *S. angusticeps* (50). *S. magnus*, the male of which is described by Tanaka (1956), and *S. angusticeps* are larger species, and the presumed male of *S. brevicaudatus* is described below. According to Brodsky (1950) the male of *S. abyssalis* is unknown, although Vervoort (1946) mentioned a male of *S. abyssalis* var. *pygmaeus* measuring 1.14 mm. Presumably the males listed by Vervoort (1957) and that described by Bradford (1971a) are too large (1.7–2.2 mm) to be *S. abyssalis*. The males of all species in which the female has a spiny cephalothorax are also unknown. The present specimens seem to be the right size to be the males of *S. abyssalis* – the females of this species here average 1.04 mm in length (1055 measured specimens), whereas those of *S. spinosus* are larger (1.79 mm from 156 specimens). They are

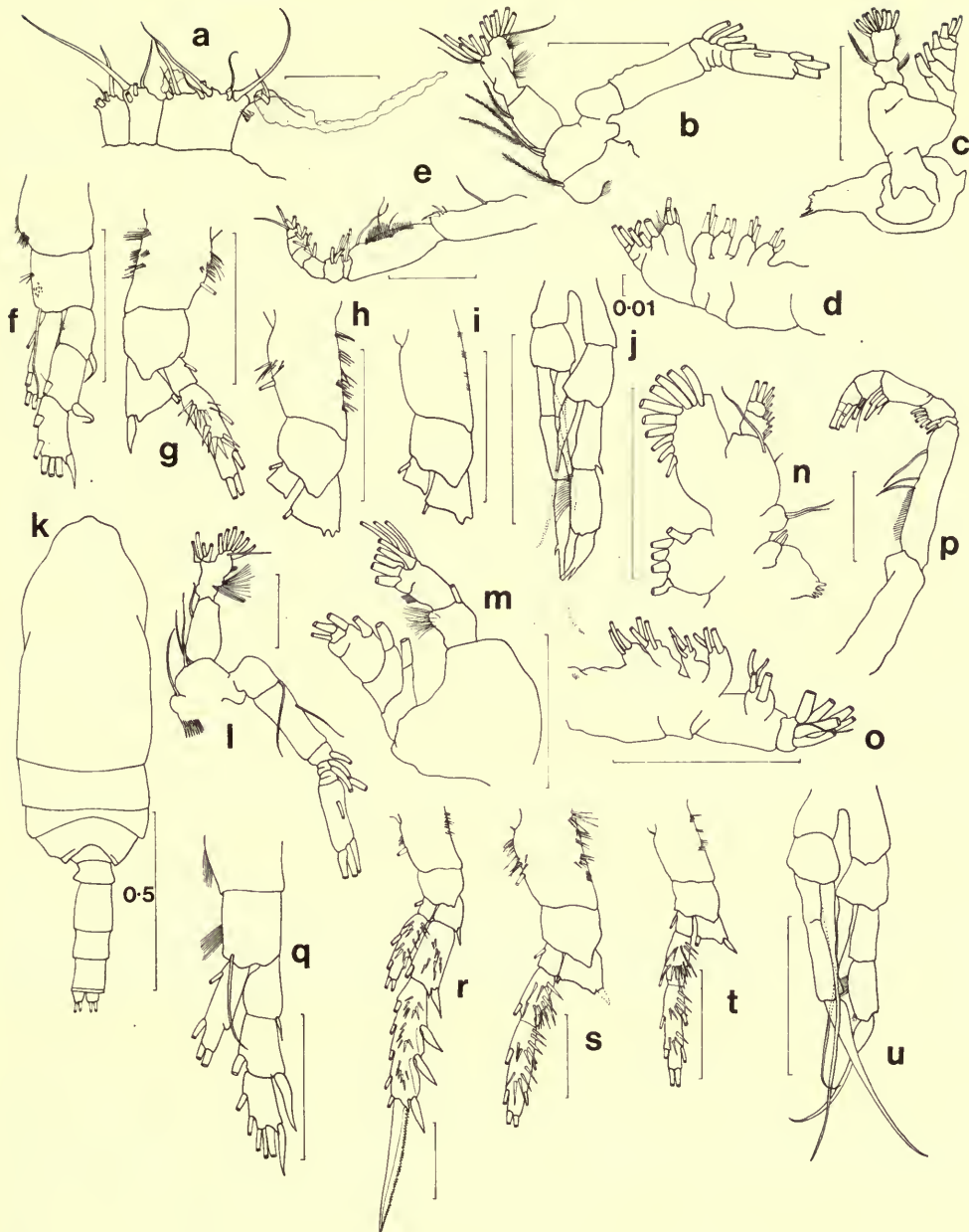


FIG. 1. a-j, *Spinocalanus? abyssalis* ♂. a, base of 1st antenna; b, 2nd antenna; c, mandible; d, 2nd maxilla; e, maxilliped; f, 1st leg; g, 2nd leg; h, 3rd leg; i, 4th leg; j, 5th leg; k-u, *Spinocalanus? brevicaudatus* ♂. k, body, dorsal; l, 2nd antenna; m, mandibular palp; n, 1st maxilla; o, 2nd maxilla; p, maxilliped; q, 1st leg; r, 2nd leg; s, 3rd leg; t, 4th leg; u, 5th leg. Bar scale 0.1 mm unless indicated.

recorded here as *S. abyssalis* although in the absence of complete animals this identification remains tentative.

Spinocalanus ? brevicaudatus Brodsky, 1950

MATERIAL EXAMINED : 21 males from 10 RMT 1 hauls made at 1250–300 m depth in a position 18°N 25°W, between 12 and 17 November 1969. 17 specimens deposited at the British Museum (Natural History), reg. no. 1974 : 483–493.

DESCRIPTION. Male (Fig. 1k–u) : Body length 1.29–1.44 mm with a mean of 1.38 mm (16 specimens). The cephalothorax is elongated and just over twice as long as the 5-segmented abdomen. The head and 1st thoracic segment are completely fused and thoracic segments 4 and 5 are partially so. In lateral view the cephalothorax is not strongly arched. The 1st antenna has 22 segments and reaches to the hind edge of the 2nd abdominal segment ; it is similar in structure to that of *S. ? abyssalis* (p. 298) but has no spines on the 1st segment. The remaining mouthparts and the legs are as shown. The 1st and 2nd maxillae and the maxilliped are weakly chitinized, and the three inner lobes of the 1st maxilla bear very rudimentary short setae. The outer edge spine of the 1st exopodite segment of the 1st leg is short. The exopodites of legs 3 and 4 are damaged in all specimens. The 5th pair of legs reaches back to the hind edge of the 2nd abdominal segment.

REMARKS. Brodsky (1950) discussed the synonymy of this species. The present males seem to agree with previous descriptions of the male of *S. brevicaudatus*, especially in their rather elongate body and structure of the 5th pair of legs. There are, however, some differences : With's (1915) specimen had more setae on all lobes of the 1st maxilla, though these are mostly rudimentary and their numbers may vary, and Sars' (1903) specimen had only two rows of spines on the 2nd endopodite segment of the 4th leg whereas the present males have three.

These specimens can be distinguished from the previous species by the slightly larger size, the shape and proportions of the body, the details of some of the mouthparts and spinulation of the swimming legs, and by the structure of the 5th legs. They are tentatively identified here as *S. brevicaudatus* although since the males of so many *Spinocalanus* spp. are unknown specific determination of these specimens is doubtful.

Spinocalanus sp. Grice & Hulsemann, 1967

MATERIAL EXAMINED : 11 males from 5 RMT 1 hauls made at 1250–800 m depth in a position 18°N 25°W, between 12 and 18 November 1969. 10 specimens deposited at the British Museum (Natural History), reg. no. 1974 : 494–504.

DESCRIPTION. Male (Fig. 2) : Body length 1.22–1.29 mm with a mean of 1.25 mm (7 specimens). The cephalothorax is 3 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are fused but thoracic segments 4 and 5 are separate. The 1st antenna has 19 segments and reaches to the hind edge of the 1st abdominal segment ; the 1st segment has no group of spines. The remaining mouthparts are as shown ; the maxillae and maxilliped are weakly chitinized.

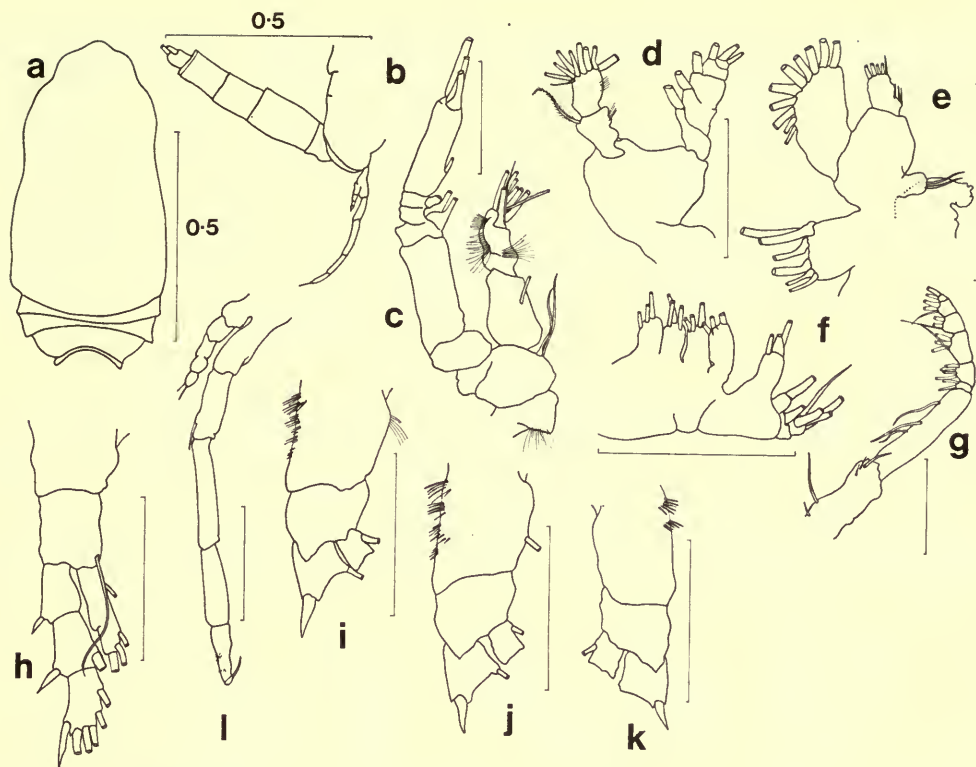


FIG. 2. *Spinocalanus* sp. ♂. a, cephalothorax, dorsal; b, abdomen and 5th legs, lateral; c, 2nd antenna; d, mandibular palp; e, 1st maxilla; f, 2nd maxilla; g, maxilliped; h, 1st leg; i, 2nd leg; j, 3rd leg; k, 4th leg; l, 5th leg. Bar scale 0.1 mm unless indicated.

Legs 2-4 are badly damaged in all the specimens. The 5th pair of legs extends back to the hind edge of the 3rd abdominal segment: the left exopodite is very long and the endopodite is reduced to a spine; the right leg is uniramous and does not reach the end of the 2nd basipodite of the left leg.

REMARKS. The present specimens seem to be conspecific with the male described as *Spinocalanus* sp. by Grice & Hulsemann (1967). They described only the 5th pair of legs of their specimen, which differs slightly from that of the present males in the relative length and segmentation of the right leg. *S. longipes* Tanaka, 1956 is similar to the present specimens but has a much longer left 5th leg. Grice & Hulsemann did not describe the length of this leg.

Spinocalanus sp. A

MATERIAL EXAMINED: 14 males from 7 RMT 1 hauls made at 1220-610 m depth in a position 18°N 25°W, between 13 and 18 November 1969. Deposited at the British Museum (Natural History), reg. no. 1974: 505-515.

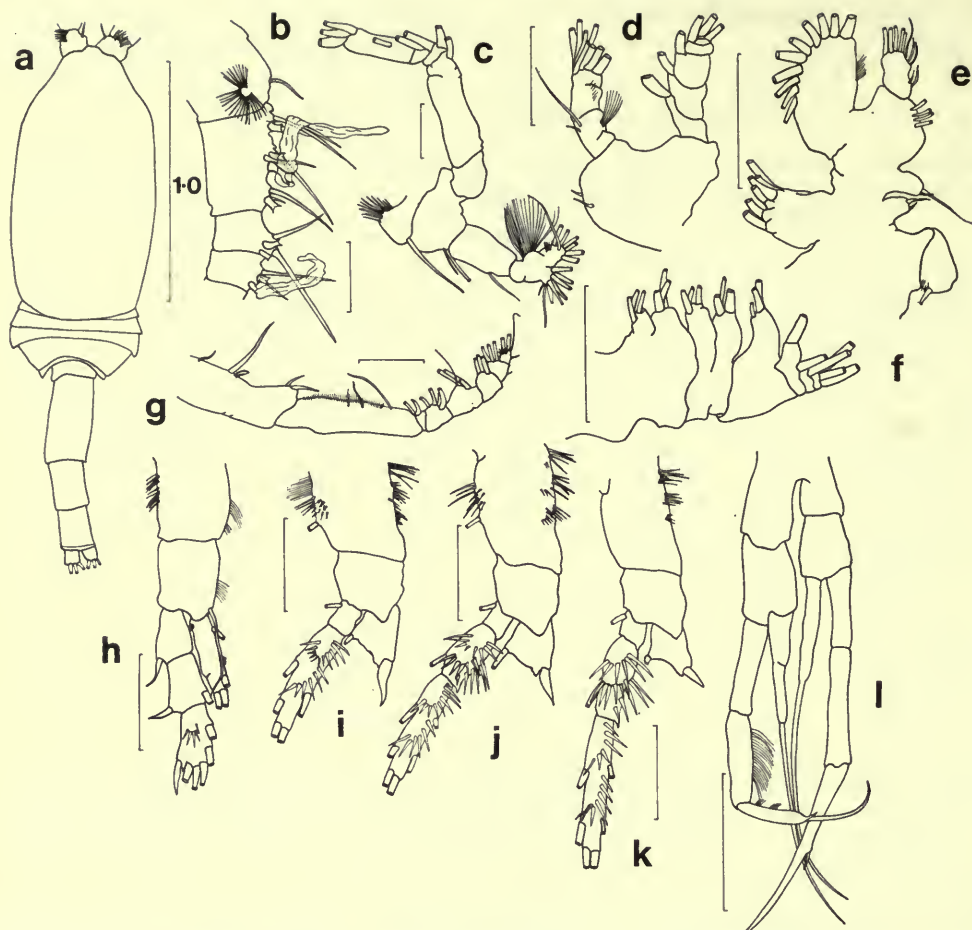


FIG. 3. *Spinocalanus* sp. A ♂. a, body, dorsal; b, base of 1st antenna; c, 2nd antenna; d, mandibular palp; e, 1st maxilla; f, 2nd maxilla; g, maxilliped; h, 1st leg; i, 2nd leg; j, 3rd leg; k, 4th leg; l, 5th leg. Bar scale 0.1 mm unless indicated.

DESCRIPTION. Male (Fig. 3): Body length 1.75–2.20 mm with a mean of 1.91 mm (11 specimens). The cephalothorax is 1.6 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are fused but thoracic segments 4 and 5 are separate. The cephalothorax is slightly arched in lateral view. The anal segment is very short and telescoped into the 4th abdominal segment. The 1st antenna has 19 segments and reaches to the hind edge of the 2nd abdominal segment; the 1st segment has a stellate group of spines on the dorsal surface and the first eight segments have large flattened sensory filaments. The remaining mouthparts and the legs are as shown. The 1st and 2nd maxillae and the maxilliped are weakly chitinized; the terminal segment of the maxilliped has a group of spines. The 3rd exopodite segment of the 1st leg has a patch of fairly large surface spines;

the exopodites of the remaining swimming legs are missing in all the specimens. The 5th pair of legs reaches back to the hind edge of the 2nd abdominal segment.

REMARKS. These specimens differ from any known *Spinocalanus* male. *S. stellatus* and *S. dorsispinosus* both have stellate bundles of spines on the 1st antenna, but the males of both species are larger than the present specimens and are structurally quite distinct. Females of *S. horridus*, *S. angusticeps*, *S. hoplites*, *S. usitatus* and *S. pteronus*, for all of which the males are unknown, were found in the same hauls as these specimens. Since they may be the undescribed male of a known species they are not considered here to be a new species.

Spinocalanus sp. B

MATERIAL EXAMINED: 2 males taken in an RMT 1 haul made at 1220–1000 m depth in a position 18°N 25°W on 18 November 1969. Deposited at the British Museum (Natural History), reg. no. 1974: 516 and 517.

DESCRIPTION. Male (Fig. 4): Body length 2.05 mm (both specimens). The cephalothorax is slightly distorted in both specimens and is about 2.6 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are fused but

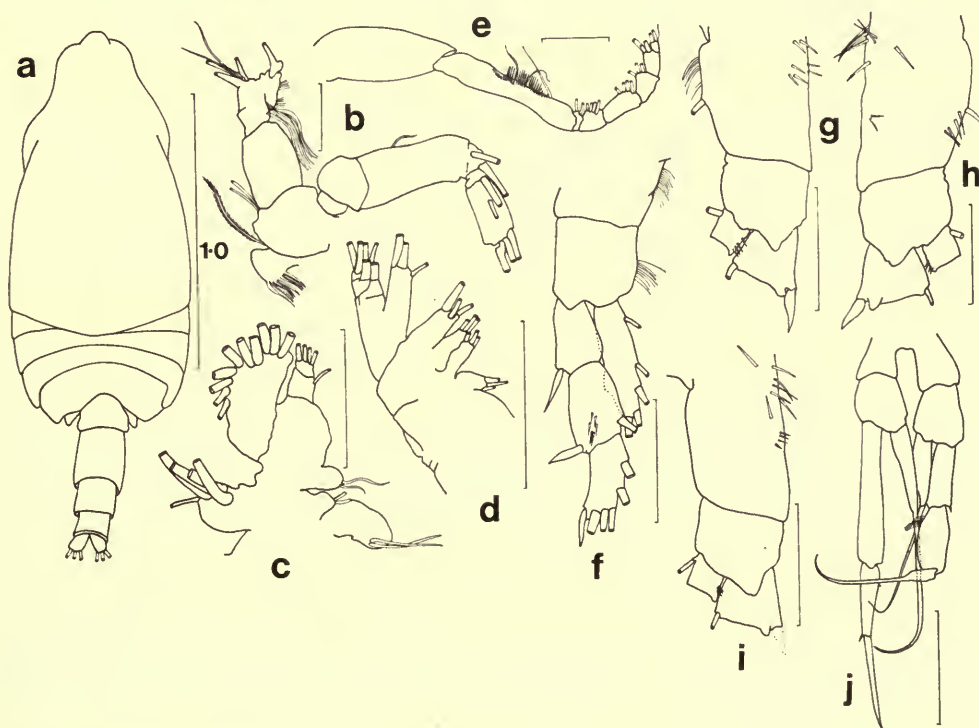


FIG. 4. *Spinocalanus* sp. B ♂. a, body, dorsal; b, 2nd antenna; c, 1st maxilla; d, 2nd maxilla; e, maxilliped; f, 1st leg; g, 2nd leg; h, 3rd leg; i, 4th leg; j, 5th leg. Bar scale 0.1 mm unless indicated.

thoracic segments 4 and 5 are separate. The forehead has a distinct dorsal protrusion. The 1st antennae are broken on both specimens; the 1st segment has no spines. The mandible is similar to that of the preceding species, and the remaining mouthparts are as shown. The 1st leg has a group of spines on the surface of the 2nd exopodite segment; legs 2-4 are badly damaged in both specimens. The 5th pair of legs reaches back to the hind edge of the 3rd abdominal segment.

REMARKS. These relatively large specimens do not agree with the description of any known *Spinocalanus* male. They were taken in a haul containing females of *S. horridus*, *S. hoplites*, *S. usitatus*, *S. angusticeps* and *S. abyssalis*. Since they may be the undescribed male of a known species they are not considered here to be a new species.

Family AETIDEIDAE

Aetideus arcuatus (Vervoort, 1949)

Snelliaetideus arcuatus Vervoort, 1949: 3-7, fig. 1; Park, 1970: 475; Bradford, 1971b: 32.

MATERIAL EXAMINED: 14 females and 1 male taken in 4 RMT 1 hauls made at 790-610 m depth in a position 18°N 25°W, between 12 and 14 November 1969. 6 females and the male deposited at the British Museum (Natural History), reg. no. 1974: 518-524.

DESCRIPTION. Female (Fig. 5a-d): Body length 1.52-1.67 mm with a mean of 1.60 mm (12 specimens). The present females agree generally with Vervoort's (1949) account but show the differences noted by Bradford (1971b). Hence the endopod of the 1st maxilla has 12 setae instead of 9, the endopodite of the 2nd leg has only one segment - but with a more or less obvious line of fusion, and there is a group of small spines at the base of the seta on the 1st basipodite of the 4th leg. The 2nd maxilla was obscure in Vervoort's specimen; it is shown here and has six fine setae on the endopodite - not five as stated by Vervoort.

Male (Fig. 5e-m): Body length 1.22 mm. The head and 1st thoracic segment are fused, as are thoracic segments 4 and 5. There is no rostrum and the hind margin of the cephalothorax is rounded. The abdomen has four segments, and the furcal rami are about 3 times longer than wide. The 1st antenna has 20 segments and reaches to the hind edge of the 2nd abdominal segment. The 2nd antenna and mandibular palp are as in the female; the mandible blade is only a simple lamella. The 1st maxilla is reduced as shown (Fig. 5j); the 2nd maxilla is very reduced, and the maxilliped is similar to that of the female but lacks setae on the 1st basipodite. The swimming legs are similar to those of the female. The endopodite of the 2nd leg has one segment but has an obvious line of fusion. There are no spines on the 1st basipodite of the 4th leg. The 5th leg is uniramous and present on the left side only. It has five segments, the last of which has patches of spinules and terminates in a group of modified setae.

REMARKS. Except for the absence of spines on the 1st basipodite of the 4th leg the present male differs from the females only in the normal sexual characters. It

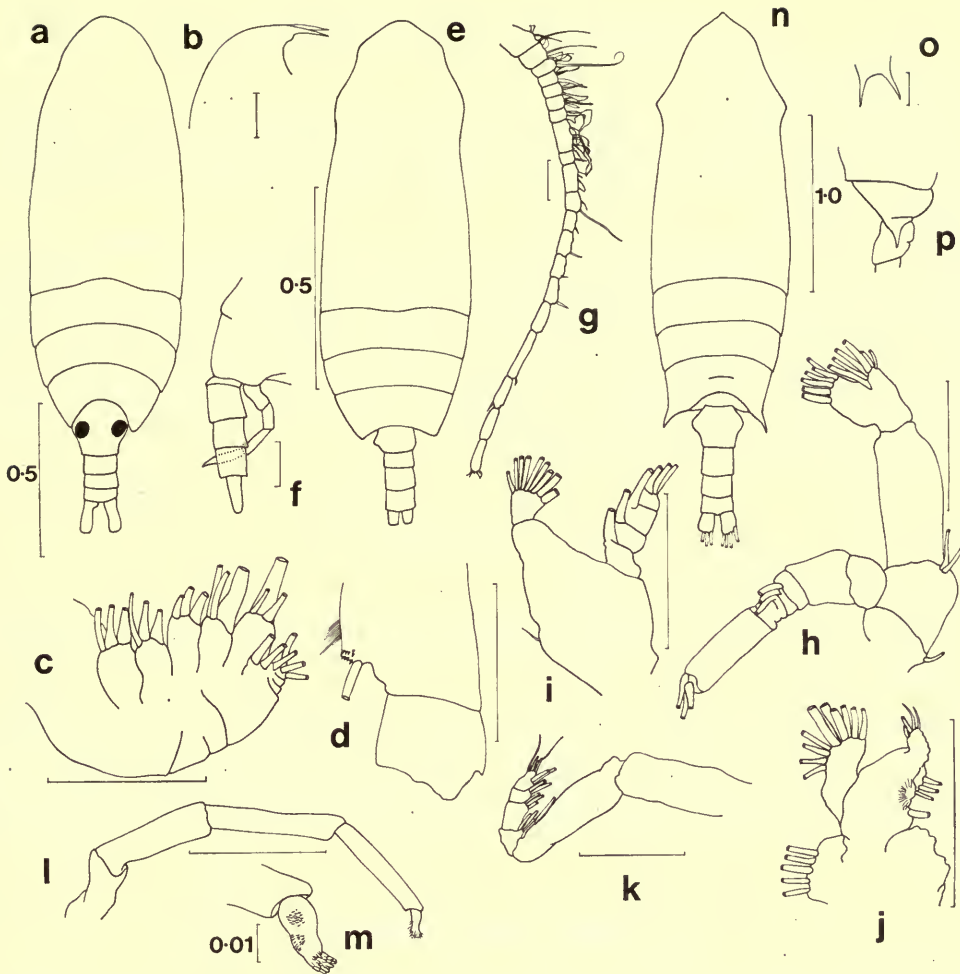


FIG. 5. a-d, *Aetideus arcuatus* ♀. a, body, dorsal; b, forehead and rostrum, lateral; c, 2nd maxilla; d, 4th leg. e-m, *Aetideus arcuatus* ♂. e, body, dorsal; f, abdomen and 5th leg, lateral; g, 1st antenna; h, 2nd antenna; i, mandibular palp; j, 1st maxilla; k, maxilliped; l, 5th leg; m, terminal segment, 5th leg. n-p, *Aetideopsis carinata* ♀. n, body, dorsal; o, rostrum; p, hind margin of cephalothorax, lateral. Bar scale 0.1 mm unless indicated.

is immediately distinguished from all the other males in the genus by having no points on the hind margin of the cephalothorax. On the basis of the females Bradford (1971b) concluded that the only difference between *Snelliaetideus* Vervoort, 1949 and *Aetideus* Brady, 1883 was the absence of postero-lateral thoracic points. This discovery of the male confirms Bradford's opinion and *Snelliaetideus* should, I believe, be amalgamated with *Aetideus*.

Aetideopsis carinata Bradford, 1969

Aetideopsis carinata ? ; Roe, 1972a : 294, 302, 308.

MATERIAL EXAMINED : 14 females taken in 10 N113H hauls made at 940–450 m depth off Fuerteventura (28°N 14°W), between 15 and 27 November 1965. 2 females taken in 2 RMT 1 hauls made at 500–410 m depth in a position 18°N 25°W on 16 November 1969.

REMARKS. The present females (Fig. 5n–p) agree completely with Bradford's (1969) account except for slight differences in the cephalothorax. The notch between the rostral points is more rounded than described by Bradford and the shoulders on the head are more pointed – in some specimens they are almost hook-like. Dr Bradford kindly sent me some specimens for comparison and there is no doubt that they are conspecific. The present specimens measure 2.66–2.96 mm with a mean of 2.79 mm (16 specimens).

Gaetanus ferox With, 1915*

Gaetanus sp. Roe, 1972a : 286, 302, 308.

MATERIAL EXAMINED : 2 males taken in 2 N113H hauls fished at 510–450 m and 300–240 m depth respectively, off Fuerteventura (28°N 14°W) on 15 and 16 November 1965.

REMARKS. These specimens conform with the descriptions of With (1915) and Grice and Hulsemann (1967). The right exopodite of the 5th leg has two segments thereby agreeing with With's account rather than Grice & Hulsemann's. The present specimens measure 3.12 and 3.27 mm and are slightly smaller than previous records.

Chiridiella ovata Deevey, 1974

? *Chiridiella macrodactyla* ; Scott, 1909 : 79, pl. 36.

MATERIAL EXAMINED : 1 female taken in an RMT 1 haul made at 1200–1000 m depth in a position 18°N 25°W on 18 November 1969.

REMARKS. I was preparing to describe this specimen as a new species until Dr G. B. Deevey kindly sent me a copy of her then unpublished manuscript on *Chiridiella* (Deevey 1974). The present female (Fig. 6) agrees almost completely with her description of *C. ovata*. The 1st maxilla, however, is variable. On the left side (Fig. 6f) the 3rd inner lobe is absent – contrasting with Deevey's specimens, and the exopodite has three setae ; on the right (Fig. 6g) the 3rd inner lobe is present and has one seta, but the exopodite has only two. The 1st maxilla of Scott's (1909) specimen differs from both this and Deevey's account. The 2nd lobe of the 2nd maxilla is very small in the present specimen, and the seta on the 1st

* Park has recently concluded that *G. ferox* is the male of *Gaetanus miles*, Giesbrecht 1888. (Park, T. S. 1975. Calanoid copepods of the genera *Gaetanus* and *Gaidius* from the Gulf of Mexico. *Bull. mar. Sci.* 25 : 9–34.)

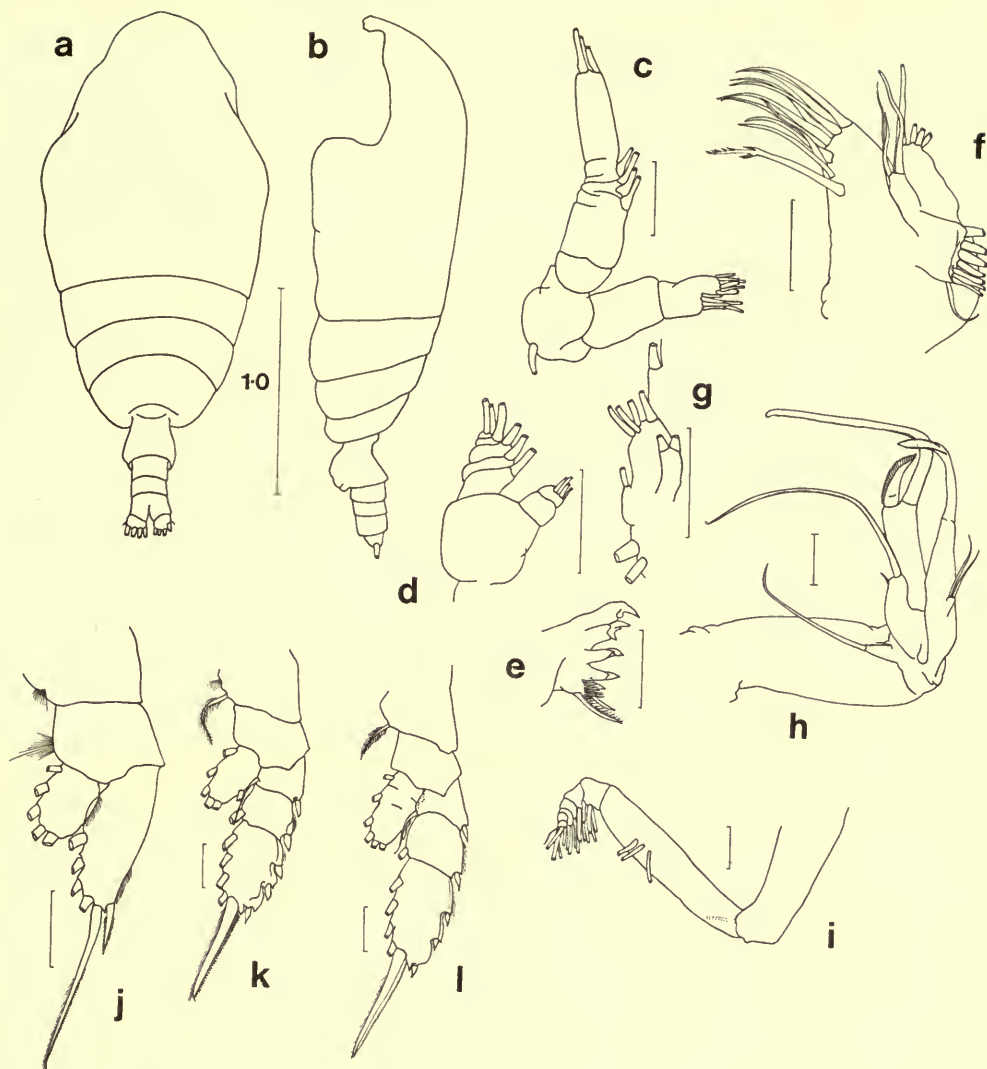


FIG. 6. *Chiridiella ovata* ♀. a, body, dorsal; b, body, lateral; c, 2nd antenna; d, mandibular palp; e, mandible blade; f, 1st maxilla, left; g, 1st maxilla, right; h, 2nd maxilla; i, maxilliped; j, 1st leg; k, 2nd leg; l, 4th leg. Bar scale 0.1 mm unless indicated.

basipodite of the maxilliped is present on one side only. The endopodites of the 3rd and 4th legs have only one segment but the lines of fusion are clearly visible.

***Pseudochirella tuberculata* Tanaka, 1957**

MATERIAL EXAMINED: 4 females and 1 male taken in 4 RMT 1 hauls made at 1250–700 m depth in a position 18°N 25°W, between 12 and 17 November 1969. The male is deposited at the British Museum (Natural History), reg. no. 1974: 525.

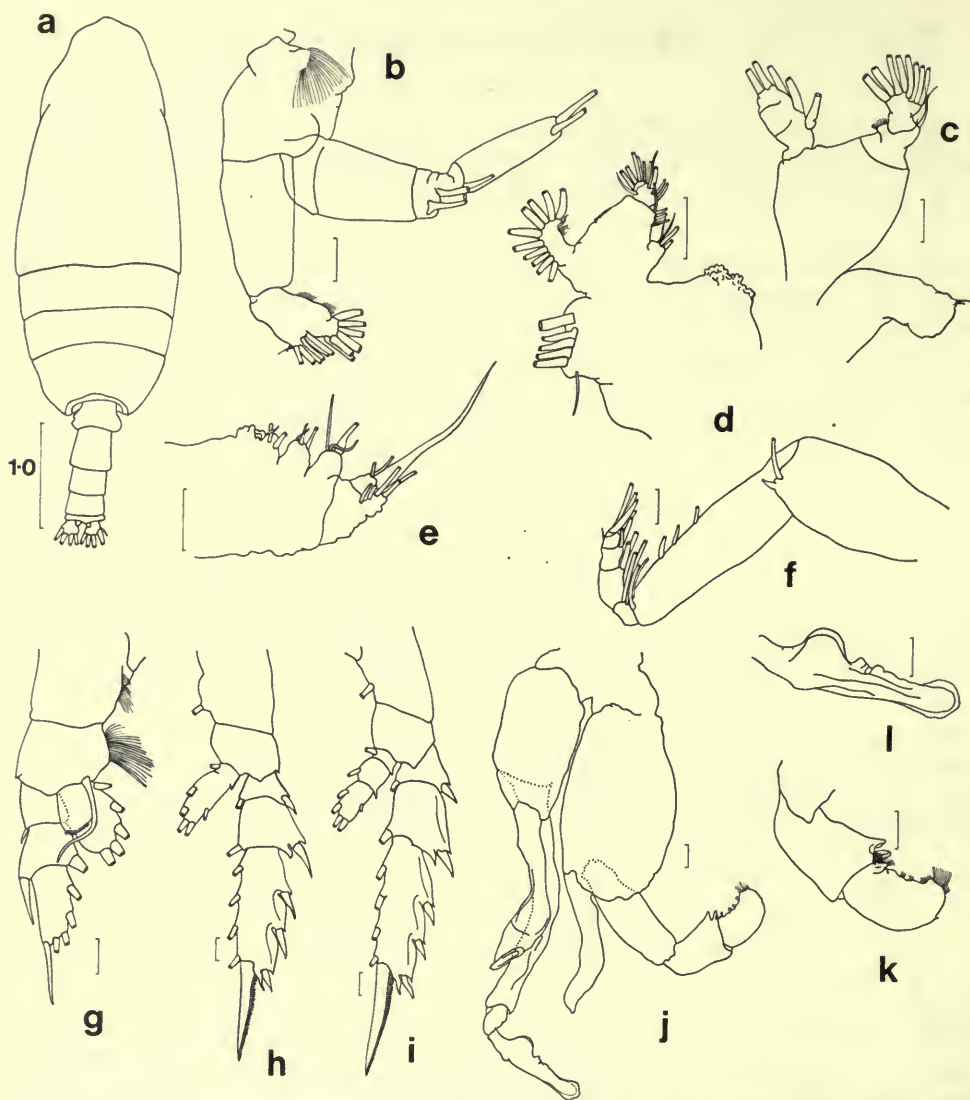


FIG. 7. *Pseudochirella tuberculata* ♂. a, body, dorsal; b, 2nd antenna; c, mandible; d, 1st maxilla; e, 2nd maxilla; f, maxilliped; g, 1st leg; h, 2nd leg; i, 4th leg; j, 5th leg; k, 5th leg, left exopodite; l, 5th leg, right 3rd exopodite segment. Bar scale 0.1 mm unless indicated.

DESCRIPTION. Male (Fig. 7): Body length 5.76 mm. The cephalothorax is robust and oval; it is 3.1 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are fused. Thoracic segments 4 and 5 are separate; the 5th segment is rounded laterally and has no spines. The rostrum is a single spike directed ventrally. The 1st antenna has 21 segments and reaches to the hind edge of the 3rd abdominal segment. The remaining mouthparts are as shown. The

exopodite of the 2nd antenna is 1.4 times as long as the endopodite. The 1st and 2nd maxillae and the mandible blade are reduced. The exopodite of the 1st leg has three segments and the endopodite has a comb of spines. The endopodite of the 2nd leg has only one segment but with an evident line of fusion; the 3rd and 4th legs have 3-segmented endopodites. The 5th pair of legs is as shown: on the left side (Fig. 7k) the 2nd exopodite segment has two strong points, and the 3rd segment is kidney-shaped with bunches of hairs; the 3rd segment of the right exopodite (Fig. 7l) has two lamellae – one on a central swelling and one terminating the segment.

REMARKS. This specimen does not fit the description of any known male *Pseudochirella*. It is nearest to Tanaka & Omori's (1969) account of *P. polyspina* Brodsky, 1950, but it is larger and differs in the detail of the mouthparts and 5th pair of legs – especially the right exopodite. It was found in association with females of *P. tuberculata* and *P. obtusa* (Sars, 1905). It does not agree with the description of the male *P. obtusa* given by Vervoort (1949). Apart from sexual characters, it differs from Tanaka's (1957) account of the female *P. tuberculata* only in the 1st leg, where his specimen had only two exopodite segments and had no comb of spines on the endopodite. The present females, however, show some variation in the degree of fusion of these exopodite segments and they do have a comb of spines. Specific attribution of *Pseudochirella* males is difficult but because the structures common to both sexes are so similar I believe that this specimen is the hitherto unknown male of *P. tuberculata*. This is the first Atlantic record of this species.

Valdiviella minor Wolfenden, 1911

? *Valdiviella brevicornis*; Scott, 1909: 78, pl. 22; Brodsky, 1950: 223, fig. 137 (male only).

MATERIAL EXAMINED: 2 females and 1 male from 2 RMT 1 hauls made at 1250–1000 m depth in a position 18°N 25°W on 17 and 18 November 1969. The male is deposited at the British Museum (Natural History), reg. no. 1974: 526.

DESCRIPTION. Male (Fig. 8): Body length 4.96 mm. The cephalothorax is 3 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are completely fused; thoracic segments 4 and 5 are partially so. The head has prominent shoulders and the rostrum has two short spikes. The hind margin of the cephalothorax is rounded laterally and has no spines. The 1st antennae are both broken off. The remaining mouthparts are identical to those described by Sewell (1929) for the male *V. insignis*. The legs are as shown. The 1st leg has three exopodite segments but the 2nd, 3rd and 4th legs have only two. The 2nd leg has a single endopodite segment and legs 3 and 4 have two endopodite segments. The exopodites and endopodites of legs 2–4 all show signs of fusion between segments. The 5th pair of legs is typical of the genus. The basipodite segments are much longer on the left side than on the right, but conversely the left endopod is much shorter than the right. The 1st and 2nd exopodite segments of the left leg each have a small spine. The 1st and 2nd exopodite segments of the right leg are partially fused and are drawn out into a long curved point.

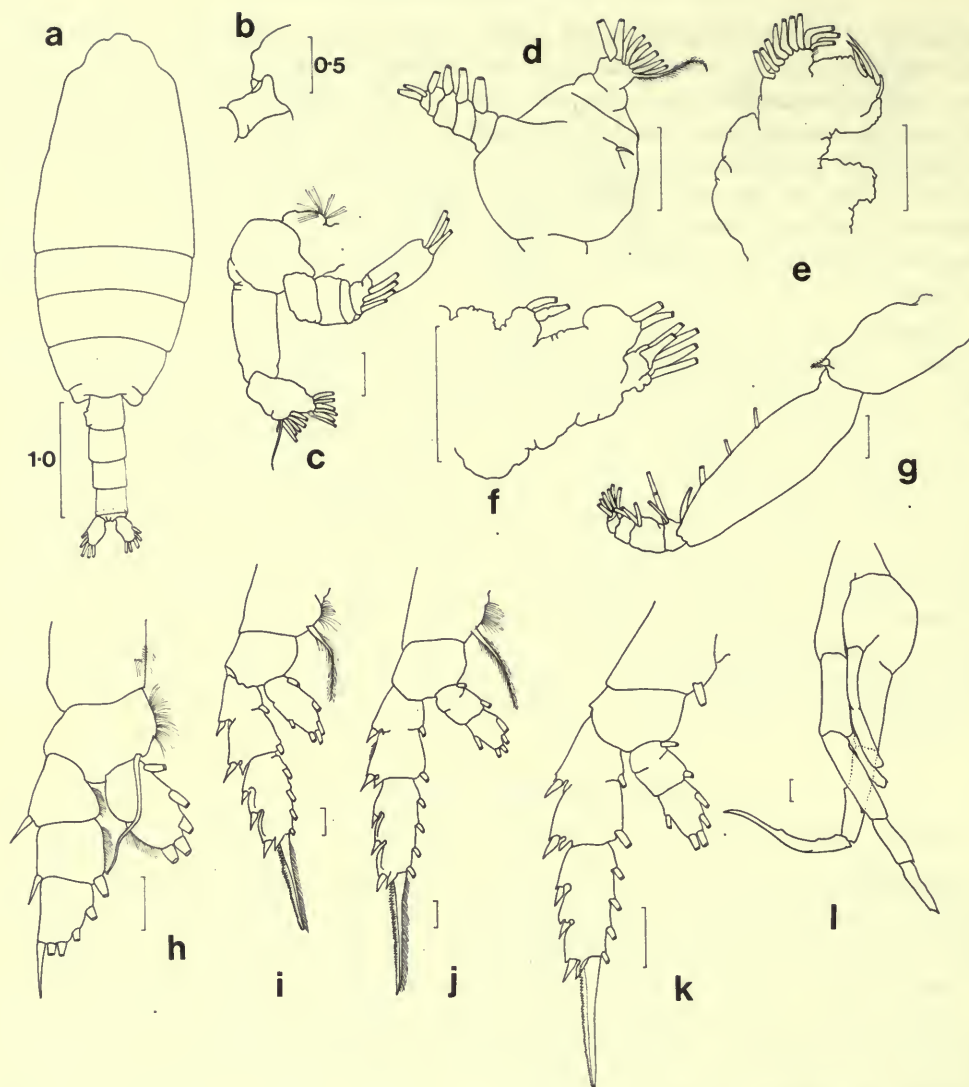


FIG. 8. *Valdiviella minor* ♂. a, body, dorsal; b, forehead and rostrum, lateral; c, 2nd antenna; d, mandibular palp; e, 1st maxilla; f, 2nd maxilla; g, maxilliped; h, 1st leg; i, 2nd leg; j, 3rd leg; k, 4th leg; l, 5th leg. Bar scale 0.1 mm unless indicated.

REMARKS. This male was found with two undoubted females of *V. minor*. Both the females have the very characteristic chitinous ridge on the dorsal side of the genital segment and are identical to the descriptions of Wolfenden (1911) and Sewell (1929). They both measure 5.44 mm and are thus slightly larger than previous records. The present male is distinguished both in structure and size from males of *V. insignis*, *V. oligarthra* and *V. ignota*. Of the three smaller species, *V. imperfecta* is very poorly known, but females of *V. brevicornis* and *V. minor* can be identified

easily. Scott (1909) described a male which he doubtfully attributed to *V. brevicornis*. Sewell (1929) also described a male as *V. brevicornis* and noted slight differences between his specimen and Scott's. Vervoort (1957) stated that Sewell's specimen(s) were 'undoubted males of *V. brevicornis*'. The present male is very similar to that described by Scott. As far as can be seen from his description it differs only in having the 4th and 5th thoracic segments and the 1st and 2nd exopodite segments of the right 5th leg partially fused instead of completely so. Sewell's specimen had a short spine on the posterior thoracic margin and a 3-segmented exopodite in the 2nd leg. I believe that Scott's male and the present specimen are conspecific. If the differences between them and Sewell's specimen of *V. brevicornis* are of specific value they may well be the hitherto undescribed male of *V. minor*, especially in view of the present association with females of this species.

Family PHAENNIDAE

Xanthocalanus agilis Giesbrecht, 1892

MATERIAL EXAMINED: 1 male taken in an RMT 1 haul made at 200–110 m depth in a position 18°N 25°W on 16 November 1969. Deposited at the British Museum (Natural History), reg. no. 1974: 527.

REMARKS. The present male (Fig. 9a–d) measures 2.58 mm and agrees with Giesbrecht's (1892) description except for the 5th pair of legs. Giesbrecht described only the elongate left leg but it is not clear from his account whether the absence of the right leg was accidental or not. Giesbrecht & Schmeil (1898) said that the right leg is absent. Other than restatements of Giesbrecht's original account I know of no other description of the male *X. agilis*. The general appearance of the present male is so similar to that of the female *X. agilis* that there can be no doubt that they are conspecific. The right leg of the 5th pair has five segments and is very short, reaching only to the end of the 1st segment of the left leg. I believe that Giesbrecht's description is incomplete and that the male *X. agilis* has a pair of 5th legs in common with other males of this genus.

Family SCOLECITHRICIDAE

Several authors have commented on the difficulties in classifying species within this large and complex family. Most recently, Bradford (1973) partially reviewed both the Phaennidae and the Scolecithricidae, redefining both families and some of their genera. Within the Scolecithricidae she found apparently consistent differences in the setation of the 1st maxilla of various genera, although the number of species which she examined was rather small. She was, however, unable to place definitely a large number of species into her redefined genera, either because of their structure or, presumably, because their descriptions are inadequate and many of their males unknown. It is therefore impossible, at the moment, to verify her narrower generic definitions for many species in this family. Re-examination of more species will clarify the acceptable limits for each genus.

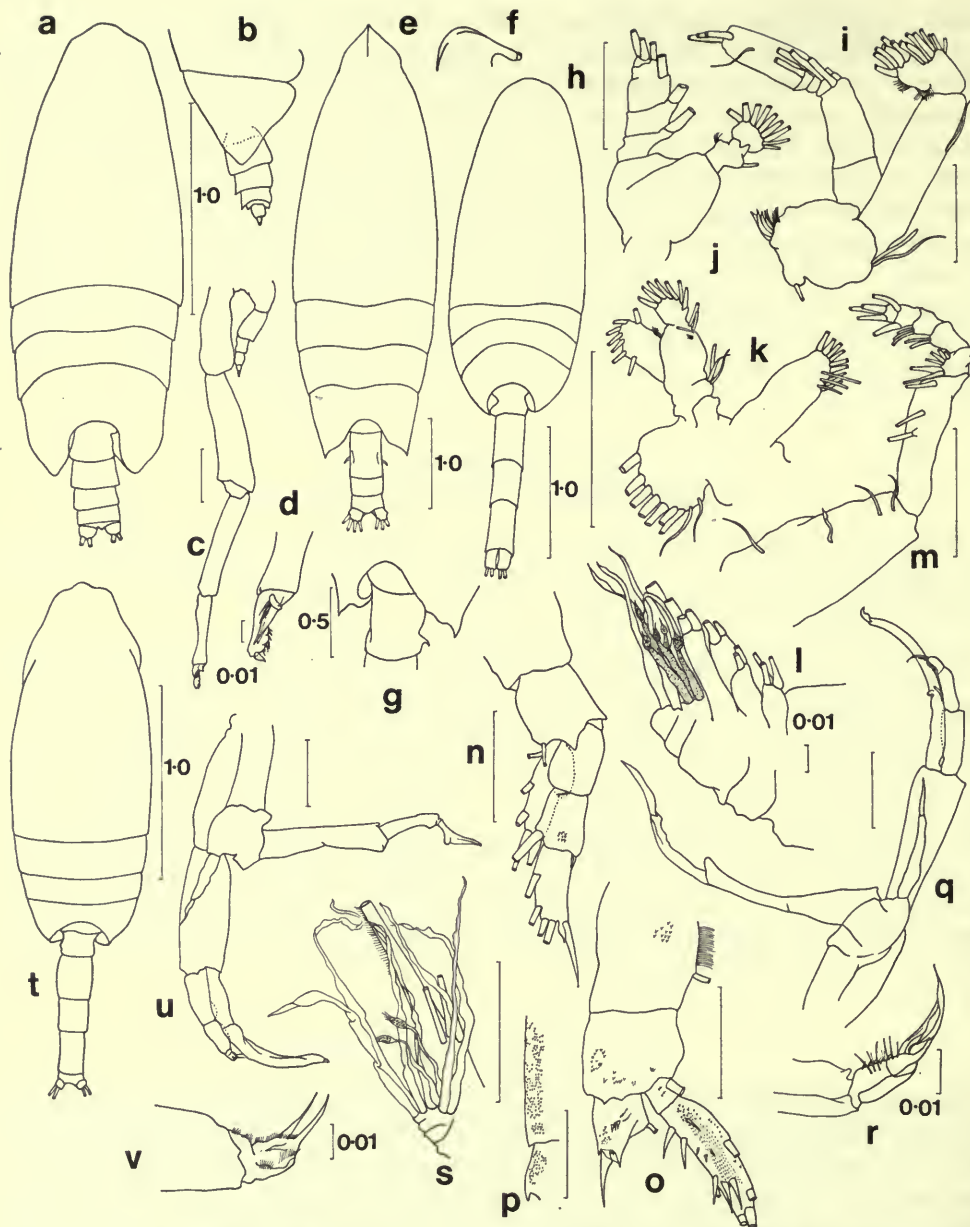


FIG. 9. a-d, *Xanthocalanus agilis* ♂. a, body, dorsal; b, last thoracic segment and abdomen, lateral; c, 5th leg; d, 5th leg, terminal segment left leg. e-g, *Scottocalanus thomasi* ♀. e, body, dorsal; f, forehead and rostrum, lateral; g, genital segment, half lateral. h-r, *Scaphocalanus* sp. ♂. h, body, dorsal; i, 2nd antenna; j, mandibular palp; k, 1st maxilla; l, 2nd maxilla; m, maxilliped; n, 1st leg; o, 2nd leg; p, 4th leg, basipodite segments; q, 5th leg; r, 5th leg, 3rd exopodite segment left leg. s, *Scolecithricella laminata* ♀, 2nd maxilla endopod. t-v, *Scolecithricella laminata* ♂. t, body, dorsal; u, 5th leg; v, 5th leg, 3rd exopodite segment left leg. Bar scale 0.1 mm unless indicated.

The present collections contain several rare and new scolecithricid species. Some of these agree well with Bradford's generic definitions but some do not. A new genus is described for some of the latter species but others are maintained within existing genera pending further study of the variation within these.

***Scottocalanus thomasi* Scott, 1909**

? *Scottocalanus backusi* Grice, 1969 : 451, figs 16–34.

MATERIAL EXAMINED : 3 females and 1 male taken in 3 RMT 1 hauls made at 500–210 m depth in a position 18°N 25°W, between 12 and 16 November 1969.

REMARKS. The present females (Fig. 9e–g) agree with Grice's (1969) description of *S. backusi* which is, in turn, very similar to *S. thomasi*. The females of these two species apparently differ only in the structure of their genital segment where *S. backusi* has a pair of spine-like protrusions. Sewell (1929), however, described the genital segment of *S. thomasi* as having 'a finger-like backwardly directed projection near the posterior margin a little to the left of the middle line'. Scott (1909) made no mention of this. (Sewell's description of three endopodite segments on the 1st maxilla of *S. thomasi* may be atypical since Scott described this as being 'nearly similar' to that of *S. securifrons* which has only two endopodite segments.) I have examined a female specimen of *S. thomasi* in the collections of the British Museum (Natural History), which was taken at 'Investigator' Station 670 and presumably identified by Sewell. It has two spine-like projections on its genital segment exactly as shown here (Fig. 9e, g). These projections are not always conspicuous, especially if they are bent back alongside the genital segment, and they can be easily overlooked, as they apparently were on this specimen. For this reason I think it probable that *S. backusi* and *S. thomasi* are conspecific. The present female specimens measure 5.92–6.08 mm and the male 5.92 mm.

***Lophothrix latipes* (T. Scott, 1894)**

MATERIAL EXAMINED : 5 females and 12 males taken in 7 NI13H hauls made at 800–90 m depth off Fuerteventura (28°N 14°W), between 13 and 28 November 1965. 13 females and 28 males taken in 9 RMT 1 hauls made at 700–49 m depth in a position 18°N 25°W, between 13 and 16 November 1969. 7 males are deposited at the British Museum (Natural History), reg. no. 1974 : 528–535.

DESCRIPTION. Male (Fig. 10) : Body length 2.96–3.19 mm with a mean of 3.05 mm (26 specimens). The cephalothorax is 3.4 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are fused ; thoracic segments 4 and 5 are separate. The head has a low crest and the forehead is angular in lateral view. The rostrum has two thick filaments. The head has prominent shoulders. The hind margin of the 1st thoracic segment is undulating and the ventro-lateral margin of the 5th thoracic segment is abruptly cut off. The 1st antenna has 20 segments and reaches to the end of the cephalothorax. The remaining mouthparts are as shown. The mandible blade, 1st and 2nd maxillae and the maxilliped are reduced.

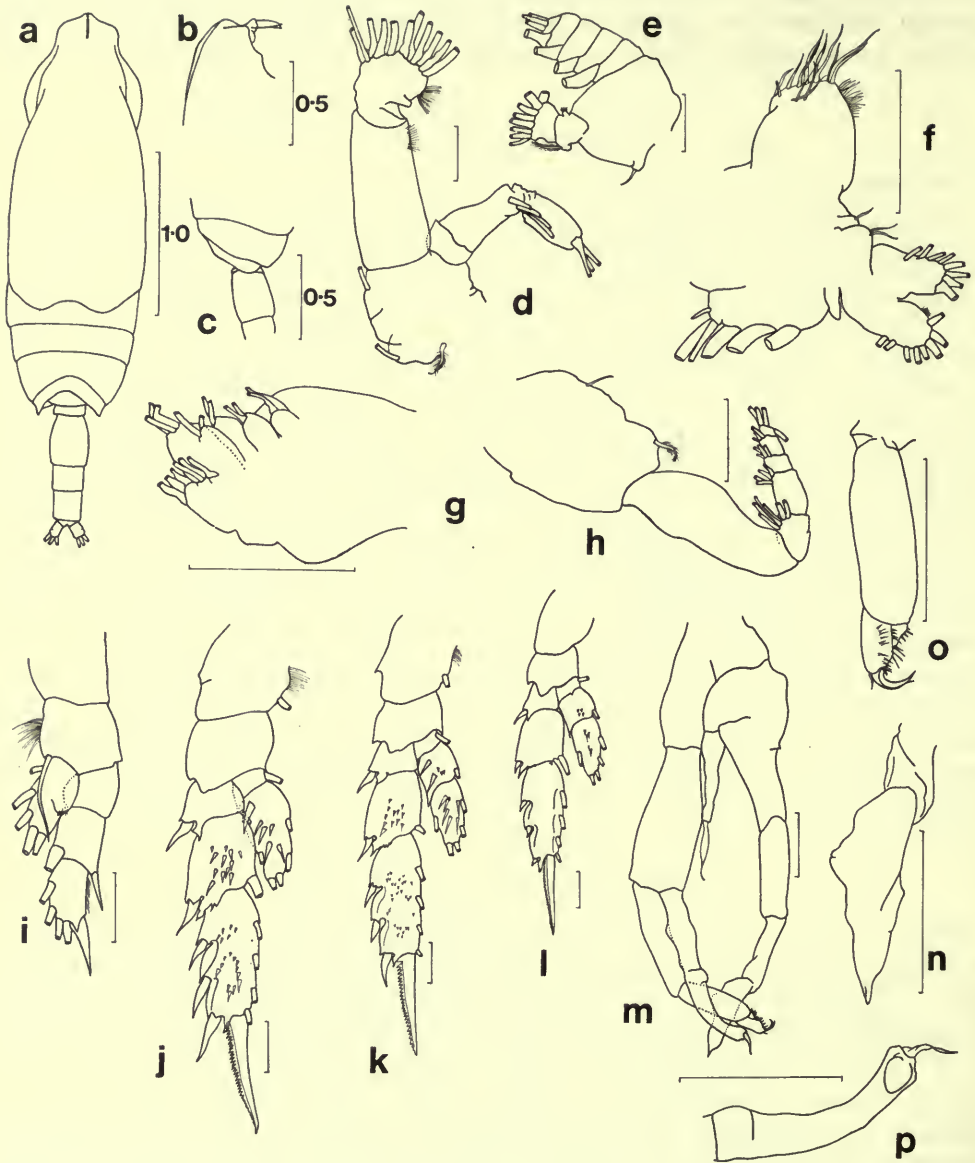


FIG. 10. *Lophothrix latipes* ♂. a, body, dorsal; b, forehead and rostrum, lateral; c, thoracic segments 4 and 5, lateral; d, 2nd antenna; e, mandibular palp; f, 1st maxilla; g, 2nd maxilla; h, maxilliped; i, 1st leg; j, 2nd leg; k, 3rd leg; l, 4th leg; m, 5th leg; n, 5th leg, last exopodite segment right leg; o, 5th leg, terminal exopodite segments left leg; p, 5th leg, last endopodite segment left leg. Bar scale 0.1 mm unless indicated.

The endopod of the 2nd maxilla has six sensory setae, none of which are brush-like. The first four pairs of legs are identical to those of the female. The 5th pair of legs are asymmetric and reach back to the hind edge of the 3rd abdominal segment. In the right leg, the exopodite has four segments, the last of which is flattened and roughly triangular in shape; the endopodite is short and has two segments. The left leg has longer basipodite segments, the exopodite has three segments and the endopodite has two; the last exopodite segment has two wide setae and numerous spines; the endopodite terminates in a ribbon-like seta.

REMARKS. Wilson (1950) described a male as *L. latipes* which differs in many respects from the present specimens, particularly in its mouthparts, which were described as 'like those of the female', and in its 5th pair of legs. There is some confusion between Wilson's description and his figures. His figure of the lateral view of the complete animal shows a distinct crest on the forehead, but he described this as 'evenly rounded with no trace of a crest'. The same figure shows a prominent spine on the posterior margin of the last thoracic segment; this is described as 'smoothly rounded' in the text. The present males are so similar to the females in all structures common to both sexes that I have no doubt that they are conspecific. The mouthparts are typically reduced but the cephalothorax, particularly the characteristic low crest and last thoracic segment, and the swimming legs, are identical to those of the female.

Scaphocalanus difficilis sp. nov.

MATERIAL EXAMINED: 64 females from 8 RMT 1 hauls made at 700–210 m depth in a position 18°N 25°W, between 12 and 17 November 1969. The holotype was caught between 600 and 515 m on 14 November 1969. Deposited at the British Museum (Natural History), holotype reg. no. 1974:536, paratypes reg. no. 1974:537–557.

DESCRIPTION. Female (Fig. 11): Body length 1.29–1.44 mm with a mean of 1.38 mm (44 specimens). The holotype measures 1.37 mm. The cephalothorax is elongate and is 3.5 times as long as the 4-segmented abdomen. The head and 1st thoracic segment are fused as are thoracic segments 4 and 5. The rostrum has two tapering filaments. The hind margin of the cephalothorax is flattened in lateral view. The abdominal segments and furcal rami have the following proportional lengths:

$$\begin{array}{ccccccc} \text{Seg. 1+2} & 3 & 4 & 5 & \text{F. rami} & & \\ 30 & : 19 & : 19 & : 13 & : 19 & = 100 \end{array}$$

The furcal rami are twice as long as wide. The 1st antenna is broken in all specimens; the near-basal segments are flattened and typical of the genus. In the 2nd antenna the endopodite is 1.4 times longer than the exopodite. In the 1st maxilla the 1st inner lobe has only two surface setae and the 3rd inner lobe has only three setae. The endopod of the 2nd maxilla has five brush-like setae, of which two are enlarged, and three flattened worm-like setae. The 1st pair of legs has no external spine on either the 1st or 2nd exopodite segments. The outer spine

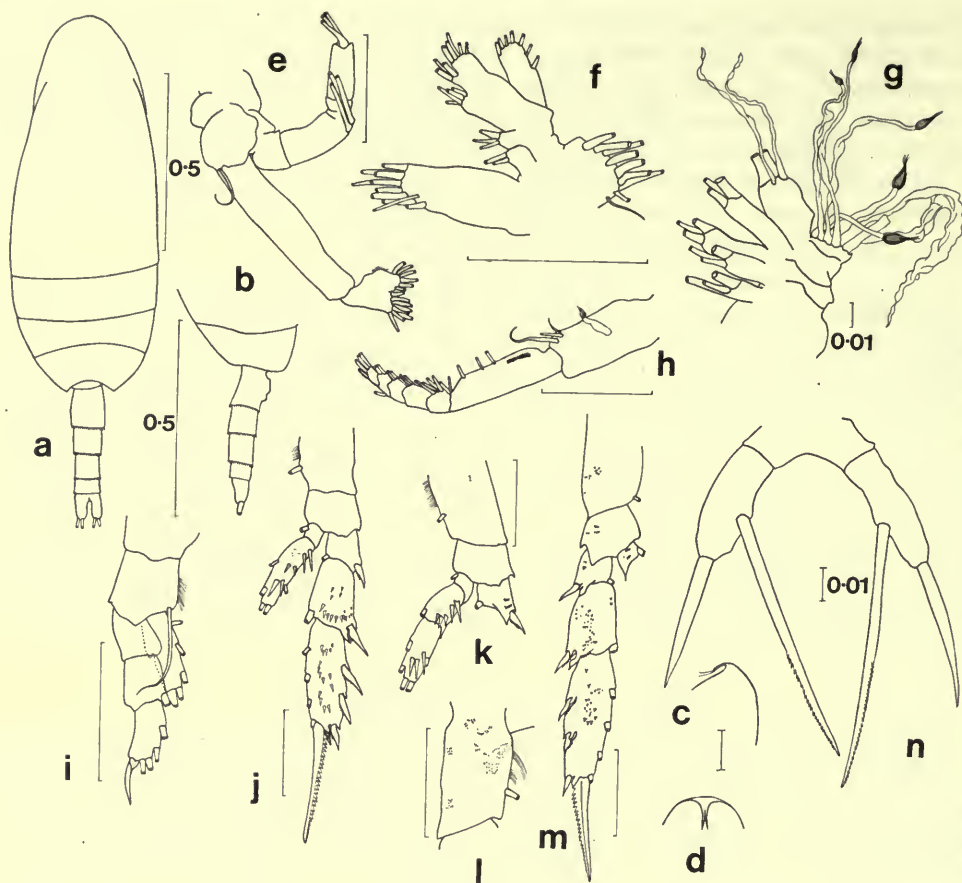


FIG. 11. *Scaphocalanus difficilis* ♀. a, body, dorsal; b, abdomen and last thoracic segment, lateral; c, rostrum, lateral; d, rostrum, ventral; e, 2nd antenna; f, 1st maxilla; g, 2nd maxilla; h, maxilliped; i, 1st leg; j, 2nd leg; k, 3rd leg; l, 3rd leg, 1st basipodite segment (paratype); m, 4th leg; n, 5th leg. Bar scale 0.1 mm unless indicated.

on the 1st exopodite segment of the 2nd leg is short. The basipodite segments of the 3rd and 4th legs have varying numbers of small surface spines. The 5th leg has a single segment on each side carrying two spines; the inner spine is 1.8 times longer than the terminal one.

REMARKS. The small size of the present species distinguishes it from all other *Scaphocalanus* species which have a well-developed 5th pair of legs. *S. longifurca* (Giesbrecht, 1888) is only slightly larger (♀ 1.48–1.90 mm – limits from Tanaka, 1961, and Grice & Hulsemann, 1965). The present species differs from Giesbrecht's (1892) description of *S. longifurca* in the following characters: (a) the endopod of the 2nd antenna longer than the exopod, (b) a relatively shorter abdomen, (c) different proportional lengths of the abdominal segments, (d) no outer spine on the 2nd

exopodite segment of the 1st leg, (e) a more or less straight outer spine on the 1st exopodite segment of the 2nd leg, and (f) different proportional lengths of the spines on the 5th leg. Giesbrecht (1892), Vervoort (1951) and Tanaka (1961) all described spines on the basal segments of legs 2-4 in *S. longifurca*. Vervoort said that these form a 'dense covering' on the 3rd leg and according to Tanaka these same joints are 'coarsely covered'. Without illustrations it is difficult to decide on the degree of spinulation in these descriptions. The present specimens have a varying number of small spines on these basal segments but they are relatively few in number. Tanaka's (1961) specimens of *S. longifurca* have the endopod of the 2nd antenna longer than the exopod, and the cephalothorax is 3.5 times as long as the abdomen. They differ from the present females, however, in the proportional lengths of the abdominal segments and in the shape of the hind margin of the cephalothorax.

S. subbrevicornis (Wolfenden, 1911) is very similar, if not identical, with *S. longifurca* (Farran, 1929; Vervoort, 1951; Tanaka, 1961). In some of the slight differences between these two species - the proportions of the rami of the 2nd antenna, the straight outer spine of the 1st exopodite segment of the 2nd leg of *S. subbrevicornis*, and the degree of spinulation of the basal joints of legs 2-4 - *S. subbrevicornis* is structurally more similar to the present species. Moreover, the relative length of the abdomen and the proportional lengths of the abdominal segments are also similar to the present females (Tanaka, 1961). *S. subbrevicornis* is, however, larger, females measuring 1.60-2.10 mm (extremes from Vervoort, 1957, and Grice & Hulsemann, 1965) and there are differences in the 1st and possibly also the 5th pair of legs.

Whether or not these slight differences merit separation into three species is questionable. It may be necessary to amalgamate two or all of them in future but for the moment at least they can remain separate. The 1st maxilla of *S. difficilis* differs from Bradford's (1973) definition of the genus in having only two surface setae on the 1st inner lobe and three setae on the 3rd inner lobe. This last character is shared with other scaphocalanids, however, e.g. *S. similis* and *S. invalidus* (Hure & Scotto di Carlo, 1968), and the general structure of the present species is so similar to *Scaphocalanus* that there can be no doubt that it belongs to this genus.

Scaphocalanus sp.

MATERIAL EXAMINED: 3 males taken in 2 RMT 1 hauls, one at 900-800 m depth and the other at 500-410 m, in a position 18°N 25°W on 14 and 16 November 1969. Deposited at the British Museum (Natural History), reg. no. 1974: 558-560.

DESCRIPTION. Male (Fig. 9h-r): Body length 1.98-2.13 mm with a mean of 2.05 mm (3 specimens). The cephalothorax is 1.9 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are completely fused, thoracic segments 4 and 5 are partially so. The rostrum has two thickened filaments. The abdominal segments and furcal rami have the following proportional lengths:

Seg.	1	2	3	4	5	F. rami	
	13	: 26	: 21	: 29	: 3	: 8	= 100

The 1st antenna has 20 segments and reaches back to the hind edge of the 2nd abdominal segment; the first eight segments have long sensory setae. The remaining mouthparts are as shown. The swimming legs are damaged in all specimens. The outer spine on the 1st exopodite segment of the 2nd leg is moderately long and straight. The basipodite segments of legs 2-4 are covered with small surface spines which are particularly dense on legs 3 and 4. The 5th pair of legs reaches back to the end of the abdomen. On the left side the exopodite is much shorter than the endopodite; the last exopodite segment has some coarse setae and a lamella, and the endopodite has no marked swelling along its length.

REMARKS. These specimens cannot be identified with any of the known *Scaphocalanus* males. The abdomen, with an unswollen 2nd segment, is similar to that described for *S. echinatus* by Tanaka (1961) but the present males are larger and have a different 5th pair of legs. As the males of several *Scaphocalanus* species are unknown and as these specimens are all damaged they cannot be described as new species.

***Scolecithricella obscura* sp. nov.**

MATERIAL EXAMINED: 10 females taken in 3 RMT 1 hauls made at 1250-800 m depth and 1 female taken in an RMT 1 haul at 500-410 m. The holotype was taken at 1250-1000 m on 16 November 1969. All hauls were made in a position 18°N 25°W, between 14 and 18 November 1969. Deposited at the British Museum (Natural History), holotype reg. no. 1974: 561, paratypes reg. no. 1974: 562-570.

DESCRIPTION. Female (Fig. 12): Body length 1.82-2.13 mm with a mean of 2.04 mm (10 specimens). The holotype measures 1.90 mm. The cephalothorax is an elongated oval, and is 5.9 times as long as the 4-segmented abdomen. The head and 1st thoracic segment and thoracic segments 4 and 5 are fused. The rostrum has two thick filaments. The hind margin of the cephalothorax is indented laterally. The genital segment is as long as the combined length of the two subsequent segments. The furcal rami are about as long as wide. The 1st antenna is broken in all specimens. The remaining mouthparts are as shown. The endopod of the 2nd maxilla has five brush-like setae, two of which are much larger than the others, and three flattened worm-like setae. In the maxilliped the 1st basipodite is about two-thirds the length of the second, and carries one brush-like and two worm-like setae. The legs are as shown. There is no external spine on the 1st exopodite segment of the 1st leg. All the outer edge spines on the exopodite segments of the 2nd leg are long. The 5th pair of legs is uniramous and symmetrical. On each side there is a single segment, incompletely divided into three, having a small external spine - which is absent on one side of one of the paratypes, a longer terminal spine and a long stout internal spine garnished with teeth.

REMARKS. This species agrees generally with *Scolecithricella* as defined by Bradford (1973). It can be distinguished from all others in the genus by its 5th pair of legs, which are more like those found in *Amallothrix* and are very similar to those of ? *Amallothrix valens* (Farran, 1926). The great development of two of the

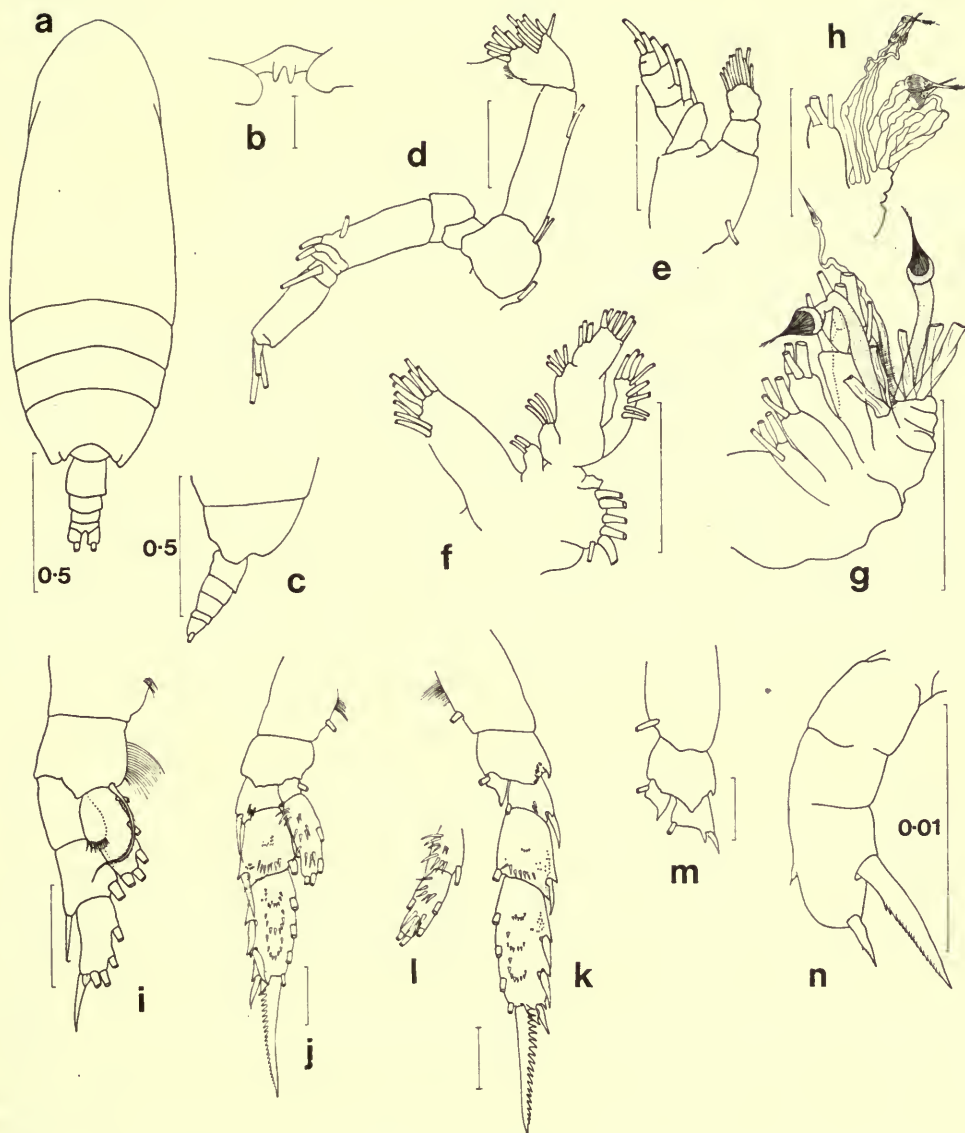


FIG. 12. *Scolecithricella obscura* ♀. a, body, dorsal; b, rostrum, ventral; c, last thoracic segment and abdomen, lateral; d, 2nd antenna; e, mandibular palp; f, 1st maxilla; g, 2nd maxilla; h, 2nd maxilla endopod (paratype); i, 1st leg; j, 2nd leg; k, 3rd leg, exopodite; l, 3rd leg, endopodite segments 2-3; m, 4th leg; n, 5th leg. Bar scale 0.1 mm unless indicated.

brush-like setae of the 2nd maxilla approaches the condition seen in *Amallothrix altera* (p. 331). Few authors have figured these setae in detail in *Scolecithricella* but in some species two of the brush-like setae are shorter and thicker than the others, though not, apparently, to the extent seen here (for example, see Rose, 1942).

***Scolecithricella laminata* (Farran, 1926)**

Scolecithrix laminata Farran, 1926 : 265, pl. 8 ; Bradford, 1973 : 143, 145.

Scolecithricella laminata ; Grice & Hulsemann, 1965 : 239, figs 148-m, 15a-j ; 1967 : 16 ;

Park, 1960 : 476 ; Wheeler, 1970 : 8 ; Roe, 1972a : 304, 310 ; 1972c : 540.

S. lamellifer Tanaka, 1962 : 78, fig. 146.

? *Amallothrix profunda* Brodsky, 1950 : 263, fig. 172 ; Bradford, 1973 : 144.

MATERIAL EXAMINED : 3 females and 1 male from an N113H haul made at 960–800 m depth off Fuerteventura (28°N 14°W) on 25 November 1965. 15 females and 3 males from 5 RMT 1 hauls made at 1250–700 m depth in a position 18°N 25°W, between 12 and 18 November 1969. 3 females and the males are deposited at the British Museum (Natural History), reg. no. 1974 : 571–577.

DESCRIPTION. Female (Fig. 9s) : Body length 1.82–2.28 mm with a mean of 1.94 mm (14 specimens). Redescription of these females is unnecessary as they generally agree with Farran's (1926) account but have the modifications described by Grice & Hulsemann (1965) and Tanaka (1962). The structure of the 1st and 2nd maxillae, however, seems in need of clarification. The 1st maxilla has the following number of setae : 5 large and 2 small on the 1st outer lobe, 8 on the exopod, 5 on the fused 2nd and 3rd endopodite segment, 2 on the 1st endopodite segment, 6 on the 2nd basipodite, 4 on the 3rd inner lobe, 2 on the 2nd inner lobe and 13 on the 1st inner lobe – of which 4 are on the surface as opposed to the edge. The 2nd maxilla (Fig. 9s) has 8 sensory setae on the endopodite of which only 2 are short and brush-like and 6 are long and worm-like.

Male (Fig. 9t–v) : Body length 2.20–2.43 mm with a mean of 2.35 mm (3 specimens). The cephalothorax is 2.3 times as long as the 5-segmented abdomen. The head and 1st thoracic segment and thoracic segments 4 and 5 are fused. The rostrum has two stout filaments. The hind margin of the cephalothorax is smoothly rounded. The 1st antenna has 19 segments and reaches to the end of the furcal rami. The remaining mouthparts are generally slightly smaller and more weakly chitinated than in the female ; their setation patterns are identical to those of the female except in the following respects. The basipodite of the mandibular palp has no setae ; in the 1st maxilla the 1st outer lobe has six large and two small setae, the exopodite has nine and the 2nd basipodite has five setae. The endopodite of the 2nd maxilla is as in the female with six long filaments and two shorter brush-like setae. In all the specimens the 2nd and 3rd exopodite segments of legs 2–4 are missing but the remainder of the swimming legs are identical to those of the female. The 5th pair of legs are asymmetrical and resemble those of *Scaphocalanus*. In the right leg the exopodite has three segments, the last of which is roughly triangular in shape. In the left leg the exopodite is much shorter than the 2-segmented

endopodite; the 3rd exopodite segment has bunches of fine hairs and two large setae.

REMARKS. Apart from the normal sexual characters these males are so similar to the females that there is no doubt that they are the same species. Brodsky's (1950) description of *A. profunda* is incomplete but the structure of the 5th pair of legs, especially the short exopodite of the left leg, is very similar to that of the present specimens.

In her review of the Scolecithricidae, Bradford (1973) could not place this species into a genus. She suggested that it may belong to *Amallothrix* or to an unnamed group typified by *Scolecithrix auropecten* Giesbrecht, 1892. The combination of six worm-like and two brush-like setae on the endopod of the 2nd maxilla would exclude this species from the Scolecithricidae as defined by Bradford. However, this definition of the 2nd maxilla would also exclude *Parascaphocalanus* Brodsky, 1955 although Bradford admits this genus to the family. In other respects the present species is a typical scolecithricid. The combination of the 2nd maxilla, a *Lophothrix*-type 1st maxilla with four surface setae on the 1st inner lobe, well-defined rostral filaments, a spine on the 1st exopodite segment of the 1st leg, and, in the male, relatively unreduced mouthparts and a *Scaphocalanus*-type 5th pair of legs, excludes this species from those genera defined by Bradford and from those not described by her. As mentioned earlier (p. 311), she had difficulty in definitely assigning a large number of species to genera, and rather than create a new monotypic genus for the present species it seems better to place it into *Scolecithricella* as defined by Sars (1902), until examination of more species clarifies the limits of any narrower generic definitions.

Scolecithricella aspinosa sp. nov.

MATERIAL EXAMINED: 9 females taken in 2 RMT 1 hauls—one fished at 1250–1000 m depth on 17 November 1969 and the other (containing the holotype) at 1220–1000 m on 18 November 1969. Both hauls were made at 18°N 25°W. Deposited at the British Museum (Natural History), holotype reg. no. 1974:578, paratypes reg. no. 1974:579–586.

DESCRIPTION. Female (Fig. 13): Body length 3.19–3.65 mm with a mean of 3.36 mm (8 specimens). The holotype measures 3.19 mm. The cephalothorax is oval and robust, and is 3.6 times as long as the 4-segmented abdomen. The head and 1st thoracic segment are completely fused, thoracic segments 4 and 5 are partially so. The forehead is rounded in lateral view; the rostrum has two filaments with thick sausage-shaped bases. The hind edge of the cephalothorax is slightly indented. The genital segment is longer than the combined length of the three subsequent segments. The furcal rami are about as long as wide. The 1st antenna has 23 segments and reaches to the end of the furcal rami. The remaining mouthparts are as shown. The exopod of the 1st maxilla has a group of spines. The endopod of the 2nd maxilla has five brush-like setae and three worm-like setae. In the holotype the worm-like setae are very wrinkled but this may

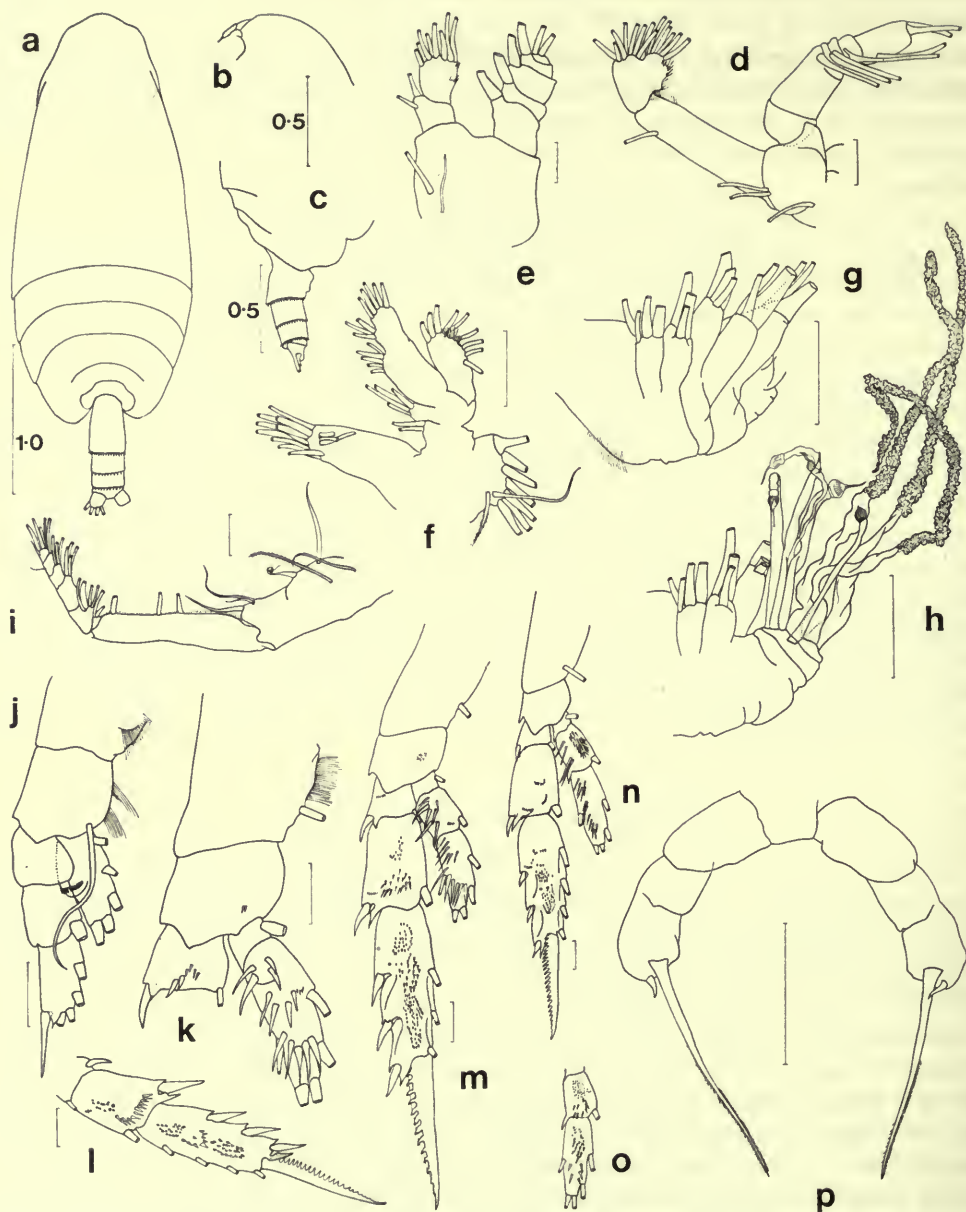


FIG. 13. *Scolecithricella aspinosa* ♀. a, body, dorsal; b, forehead and rostrum, lateral; c, last thoracic segment and abdomen, lateral; d, 2nd antenna; e, mandibular palp; f, 1st maxilla; g, 2nd maxilla, exopod; h, 2nd maxilla, endopod; i, maxilliped; j, 1st leg; k, 2nd leg; l, 2nd leg, exopodite segments 2-3 (paratype); m, 3rd leg; n, 4th leg; o, 4th leg endopod anterior surface; p, 5th leg. Bar scale 0.1 mm unless indicated.

be an artifact of preservation as in one of the paratypes these setae are simple flattened filaments. The basal segment of the maxilliped has one brush-like and two worm-like setae. The legs are as shown. The 1st leg has no outer spine on either the 1st or 2nd exopodite segment. In the 2nd leg the external spine of the 1st exopodite segment is short, and the 2nd endopodite segment has a raised lobe carrying four spines. The endopods of legs 2-4 all have long spines on their posterior surfaces; their anterior surfaces generally have small spines but those on the 4th leg are fairly large. The 5th leg is symmetrical and uniramous. On each side there are two segments with the second having a distinct line of fusion and carrying a short terminal spine and a very long internal spine.

REMARKS. *Scolecithricella aspinosa* and the following species are distinct in having no external spines on the 1st and 2nd exopodite segments of the 1st leg. Discussion of the affinities of both these species follows the description of *Scolecithricella canariensis* on p. 325.

***Scolecithricella canariensis* sp. nov.**

Scolecithricella sp. 3 Roe, 1972a : 304, 310; 1972c : 540.

MATERIAL EXAMINED : 2 females from 2 N113H hauls made at 960-825 m depth off Fuerteventura (28°N 14°W) on 25 and 27 November 1965. 9 females from 6 RMT 1 hauls made at 1220-610 m depth in a position 18°N 25°W, between 12 and 18 November 1969. The holotype was taken at 790-700 m on 12 November 1969. Deposited at the British Museum (Natural History), holotype reg. no. 1974 : 587, paratypes reg. no. 1974 : 588-597.

DESCRIPTION. Female (Fig. 14) : Body length 3.12-3.42 mm with a mean of 3.30 mm (11 specimens). The holotype measures 3.19 mm. The cephalothorax is elongate and 5.1 times as long as the 4-segmented abdomen. The head and 1st thoracic segment are fused, as are thoracic segments 4 and 5. The forehead is somewhat angular in dorsal view. The rostrum has two fairly long filaments. The hind margin of the cephalothorax is indented laterally. The genital segment is a little longer than the subsequent segment; the furcal rami are slightly longer than wide. The 1st antenna has 23 segments, the last of which extends past the furcal rami. The remaining mouthparts are as shown. The endopod of the 2nd maxilla has three ribbon-like setae and four brush-like setae. The basal segment of the maxilliped has two worm-like and one brush-like seta. The legs are as shown. The 1st leg has no external spine on either the 1st or 2nd exopodite segment. The 2nd leg has a short outer edge spine on the 1st exopodite segment and a distinct raised lobe bearing six spines on the 2nd endopodite segment. The 5th pair of legs is symmetrical and uniramous. On each side there is a single segment, which bears traces of fusion, attached to a common basal segment. Each terminal segment has a short end spine and a longer robust internal spine armed with short teeth.

REMARKS. *Scolecithricella canariensis* and *S. aspinosa* are closely related. Both have (a) no trace of an external spine on the 1st and 2nd exopodite segments of the 1st leg, (b) a *Lophothrix*-type 1st maxilla, (c) uniformly small heads to the brush-like

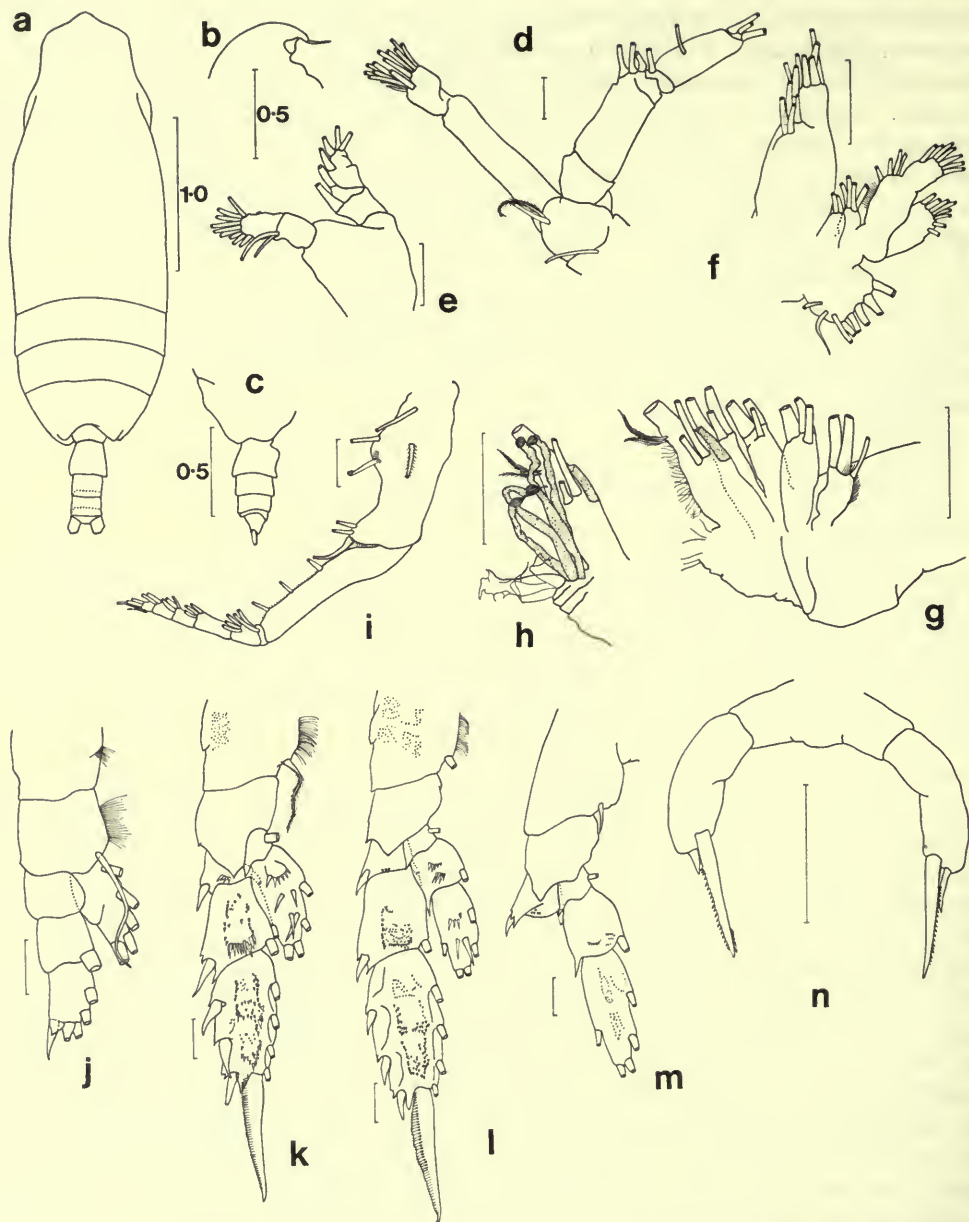


FIG. 14. *Scolecithricella canariensis* ♀. a, body, dorsal; b, forehead and rostrum, lateral; c, last thoracic segment and abdomen, lateral; d, 2nd antenna; e, mandibular palp; f, 1st maxilla; g, 2nd maxilla, exopod; h, 2nd maxilla, endopod; i, maxilliped; j, 1st leg; k, 2nd leg; l, 3rd leg; m, 4th leg; n, 5th leg. Bar scale 0.1 mm unless indicated.

setae of the 2nd maxilla (*S. canariensis* apparently only has four of these setae), (d) a similar-shaped maxilliped, and (e) a short external spine on the 1st exopodite segment of the 2nd leg and, in the same limb, a raised lobe on the 2nd endopodite segment. The two species are clearly distinct, however, differing from each other in body shape, the detailed setation of the 1st maxilla and the structure of the legs. They both show similarities with *Scaphocalanus bogorovi* Brodsky, 1955. The exopodite of the 1st leg is identical (see Grice & Hulsemann, 1965), and the maxilliped and the endopod of the 2nd maxilla are also very similar. There are differences, however, in the structure of the 1st maxilla and in the legs. *S. bogorovi* seems at best a very peculiar *Scaphocalanus* and should probably be removed from this genus.

As with *S. laminata* (p. 321) it is impossible to place either of the two present species into any of the scolecithricid genera defined by Bradford (1973), or into any of the remaining genera in this family. Both have some affinity to *Lophothrix* but also show a general resemblance to *Amallothrix*. The peculiar structure of their 1st leg, however, is constant in all the present specimens and it may be necessary to establish a new genus for these species and also perhaps for *S. bogorovi*. Pending the discovery of the males and determination of the acceptable limits within each genus both species are temporarily placed within *Scolecithricella* Sars, 1902.

Amallothrix falcifer (Farran, 1926)

Scolecithrix falcifer Farran, 1926 : 262, pl. 8 ; Bradford, 1973 : 143.
Scolecithricella sp. 2 Roe, 1972a : 296, 304, 310 ; 1972c : 540.

MATERIAL EXAMINED : 11 females and 2 males taken in 10 N113H hauls made at 960–510 m depth off Fuerteventura (28°N 14°W), between 24 and 28 November 1965. 10 females and 7 males taken in 7 RMT 1 hauls made at 1250–700 m depth in a position 18°N 25°W, between 12 and 17 November 1969. One female and 5 males are deposited at the British Museum (Natural History), reg. no. 1974 : 598–603.

DESCRIPTION. Female (Fig. 15a–m) : Body length 1.82–2.20 mm with a mean of 2.00 mm (20 specimens). The cephalothorax is oval and robust ; it is 3.8 times as long as the 4-segmented abdomen. The head and 1st thoracic segment are fused, as are thoracic segments 4 and 5. The forehead is rounded, the two rostral filaments are thickened over most of their length. The hind margin of the cephalothorax is slightly indented. The genital segment is almost as long as the combined length of the three subsequent segments. The furcal rami are only slightly longer than wide. The 1st antenna has 23 segments and reaches back to the anal segment. The maxilliped has a sensory seta in the middle of the 1st basipodite. The remaining mouthparts are as shown. The 2nd maxilla has five brush-like setae on the endopodite and at least two ribbon-like setae. The legs are as shown. The internal edge of the 2nd basipodite of the 2nd leg has a characteristic group of spines. The surfaces of legs 2 and 3 are heavily ornamented with spines.

Male (Fig. 15n–r) : Body length 1.98–2.81 mm with a mean of 2.50 mm (9 specimens). The cephalothorax is 3 times longer than the 5-segmented abdomen.

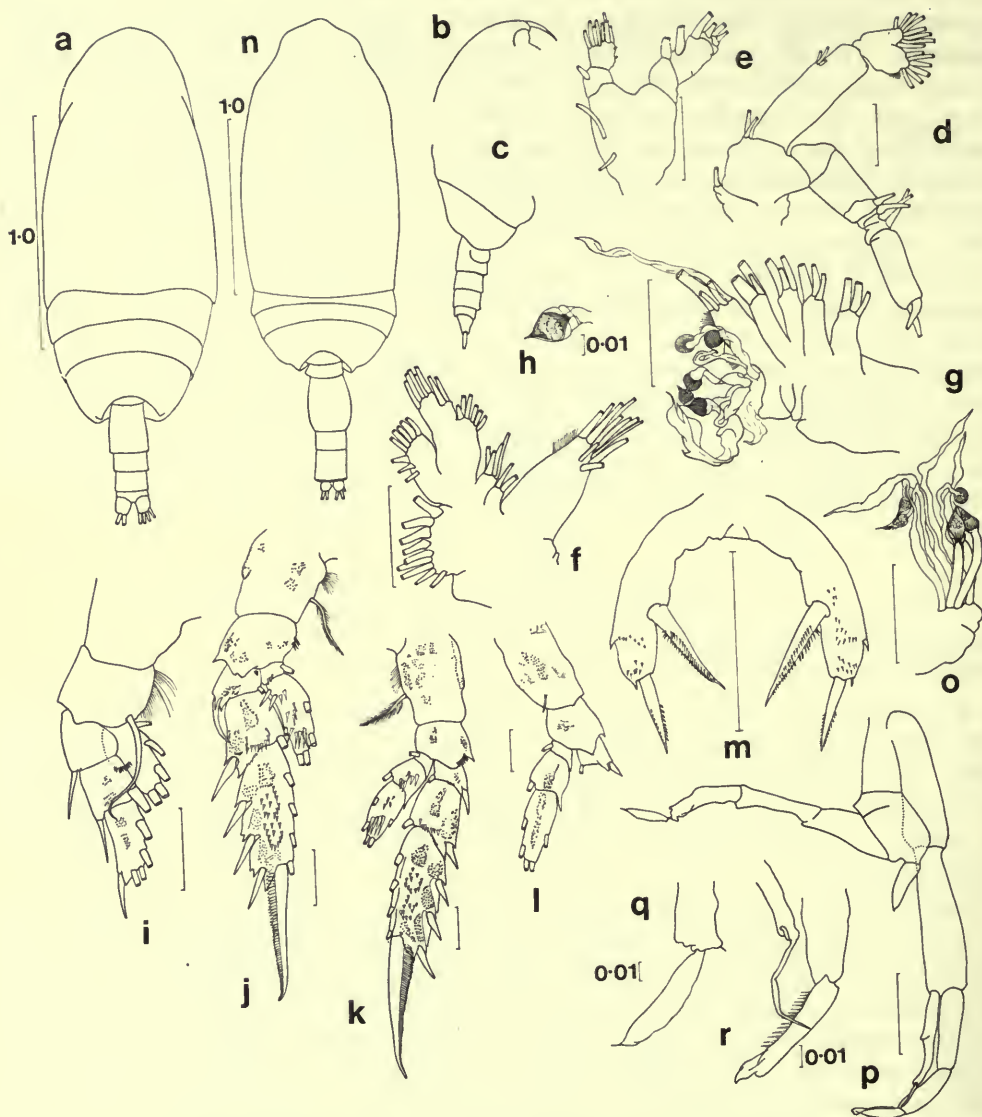


FIG. 15. a-m, *Amallothrix falcifer* ♀. a, body, dorsal; b, forehead and rostrum, lateral; c, last thoracic segment and abdomen, lateral; d, 2nd antenna; e, mandibular palp; f, 1st maxilla; g, 2nd maxilla; h, 2nd maxilla, brush-like seta head; i, 1st leg; j, 2nd leg; k, 3rd leg; l, 4th leg; m, 5th leg. n-r, *Amallothrix falcifer* ♂. n, body, dorsal; o, 2nd maxilla, endopod; p, 5th leg; q, 5th leg, last exopodite segment right leg; r, 5th leg, terminal segments left leg. Bar scale 0.1 mm unless indicated.

The head and 1st thoracic segment and thoracic segments 4 and 5 are fused. The anal segment is very short. The 1st antenna has 19 segments and reaches back to the hind edge of the 3rd abdominal segment. The setation of the mouthparts is identical to that of the female except in the following respects. In the 2nd antenna the exopodite has three terminal setae and the 1st endopodite segment has a bunch of hairs. The 1st maxilla is slightly variable; in one specimen the 1st outer lobe has eight setae, in another the 3rd inner lobe has three, and in both the 2nd basipodite has five and the 1st endopodite has three setae. In the 2nd maxilla lobes 2-5 each has an enlarged seta typical of other *Amallothrix* males and the endopodite has five brush-like setae and three ribbon-like setae. Two of the brush-like setae are short and one of these is conspicuously larger than the others. The swimming legs are identical to those of the female. The 5th pair of legs reaches back to the end of the abdomen. On the right leg the endopod is a short single segment and the last exopodite segment is leaf-shaped. On the left leg the endopod ends in a flagellum and the 3rd exopodite segment has a row of setae and a lamella.

REMARKS. *A. falcifer* is difficult to recognize from Farran's (1926) account and apart from Wilson's (1950) figure of the female 5th legs it has never been redescribed. I have compared the present material with the type specimen held in the British Museum (Natural History). The 1st maxilla of the type is not mounted and the endopodite of the 2nd maxilla is rather obscure - it does, however, have at least four brush-like setae and three ribbon-like setae. In all other respects the present females are identical to the type. The 2nd leg of Farran's specimen has the characteristic group of spines on the 2nd basipodite although this is neither described nor figured by him. Apart from sexual characters and the slightly variable setation of some of the mouthparts the males are identical to the females. They have the distinct group of spines on the 2nd basipodite of the 2nd leg. There are, apparently, two size groups in the males. Two specimens each measured 1.98 mm but the remaining seven were between 2.58 and 2.81 mm in length. There are no structural differences between the large and small specimens and both are considered to be conspecific. *Scolecithricella denticulata* Tanaka, 1962 has a similar group of spines on the basipodite of the 2nd leg but its 5th pair of legs differs from the present males. Bradford (1973) could not definitely place *A. falcifer* into *Amallothrix* following her revision of the Scolecithricidae. The present specimens are in complete agreement with her definition of this genus.

Amallothrix sp.

MATERIAL EXAMINED: 6 males from 5 RMT 1 hauls made at 1220-610 m depth in a position 18°N 25°W, between 12 and 18 November 1969. Deposited at the British Museum (Natural History), reg. no. 1974: 604-609.

DESCRIPTION. Male (Fig. 16): Body length 2.05-2.81 mm with a mean of 2.43 mm (5 specimens). The cephalothorax is 2.5 times as long as the 5-segmented abdomen. The head and 1st thoracic segment and thoracic segments 4 and 5 are fused. The rostrum has two stout filaments. The 1st antenna has 19 segments and reaches to the hind edge of the 2nd abdominal segment. The remaining mouthparts

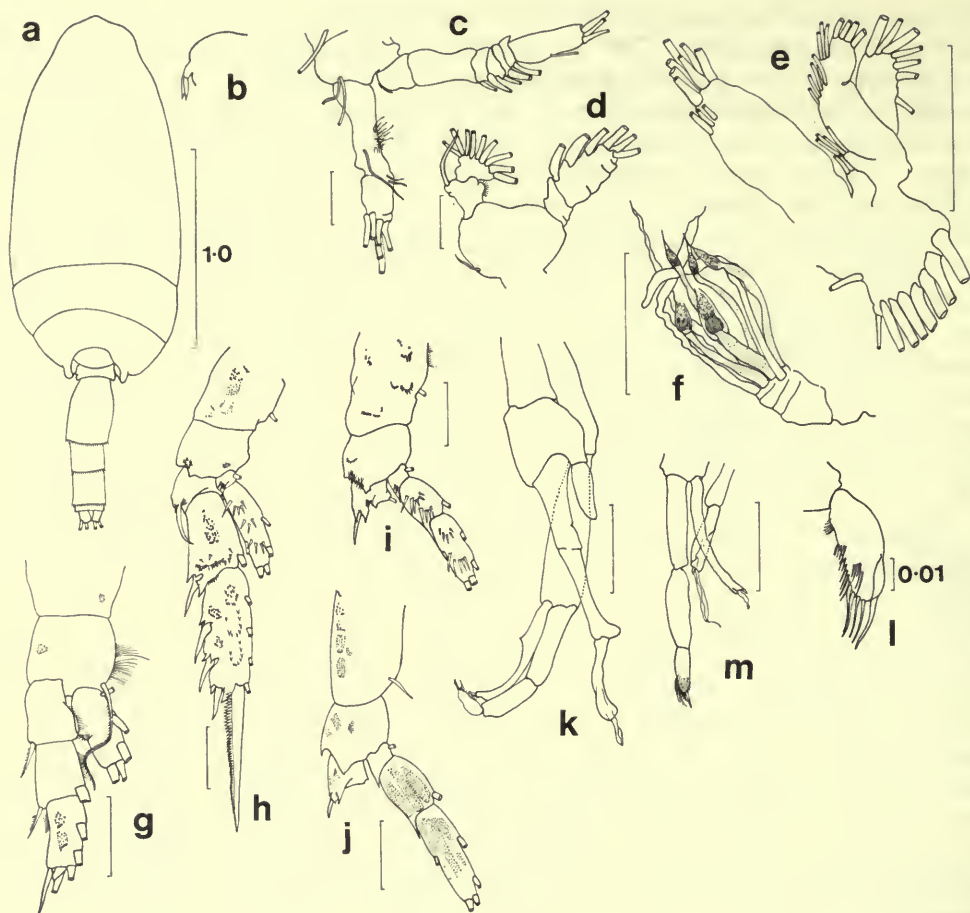


FIG. 16. *Amallothrix* sp. ♂. a, body, dorsal; b, forehead and rostrum, lateral; c, 2nd antenna; d, mandibular palp; e, 1st maxilla; f, 2nd maxilla, endopod; g, 1st leg; h, 2nd leg; i, 3rd leg; j, 4th leg; k, 5th leg; l, 5th leg, last exopodite segment left leg; m, 5th leg, terminal segments (different specimen). Bar scale 0.1 mm unless indicated.

are as shown. There is some slight variation in setation of the 1st maxilla where one specimen has nine setae on the exopodite. The swimming legs are incomplete in all specimens. The 3rd exopodite segment of the 1st leg has surface spines; the 1st exopodite segment of the 2nd leg has a long curved outer spine. The basipodites of legs 2-4 are covered with surface spines. The 5th pair of legs reaches back about half the length of the abdomen. On the left side the exopodite is slightly longer than the endopodite and the last exopodite segment has a lamella and groups of coarse setae.

REMARKS. I cannot definitely identify these specimens with any of the known males of *Amallothrix*. They show a general similarity to the male of *Amallothrix*

propinqua, described by Tanaka (1962), but differ in the spinulation of the swimming legs and in the structure of the 5th pair of legs. They agree with Bradford's (1973) redefinition of *Amallothrix*, but as they may be the undescribed male of a known species they are not considered here to be a new species.

Amallothrix lobophora (Park, 1970)

Scolecithricella lobophora Park, 1970 : 511, figs 188–201.

MATERIAL EXAMINED : 11 females and 4 males taken in 8 RMT 1 hauls made at 785–300 m depth in a position 18°N 25°W, between 13 and 17 November 1969. 2 females and the males are deposited at the British Museum (Natural History), reg. no. 1974 : 610–615.

DESCRIPTION. Male (Fig. 17) : Body length 1.44–1.67 mm with a mean of 1.56 mm (4 specimens). The cephalothorax is 2.8 times as long as the 5-segmented abdomen. The head and 1st thoracic segment and thoracic segments 4 and 5 are fused. The forehead is flattened anteriorly in dorsal view ; the rostrum has two large swollen filaments. The hind margin of the cephalothorax is bluntly triangular in lateral view. The anal segment is very short and is telescoped into the 4th abdominal segment. The 1st antenna has 19 free segments and reaches to the hind end of the abdomen ; the proximal segments have large sensory filaments. The mandible blade is similar to that of the female but smaller. The 2nd maxilla has five exopodite lobes but two have been omitted in Fig. 17h for clarity ; the endopodite has five brush-like setae, two of which have enlarged heads, and three worm-like setae. The other mouthparts and the legs are as shown. The external spine on the 2nd exopodite segment of the 1st leg varies slightly in length ; in another specimen it is longer than shown here. The 5th pair of legs is biramous and reaches back to the end of the abdomen. It is similar to that found in *Scaphocalanus* with the left endopodite longer than the exopodite. The left exopodite terminates in a lamella, which is broken in the illustrated specimen, and the last endopodite segment is knobbled. In the right leg the last exopodite segment is roughly triangular in shape.

REMARKS. These males were taken in the same hauls as several female *A. lobophora*. The present females agree with Park's (1970) description except that the 1st inner lobe of the 1st maxilla has three surface setae and not two. Some of the male mouthparts are reduced but the characteristic rostrum and the swimming legs are identical to those of the female.

Bradford (1973) transferred this species from *Scolecithricella* Sars, 1902 to *Amallothrix* Sars, 1925. The present specimens differ from her redefinition of *Amallothrix* in having a *Scaphocalanus*-type 1st maxilla with three surface setae on the 1st inner lobe. The 5th legs of both sexes also seem to be atypical of this genus and are very similar to those of *Amallothrix auropecten* (Giesbrecht, 1892). A discussion of the possible affinities of these two species is given after the account of *A. auropecten* on p. 334.

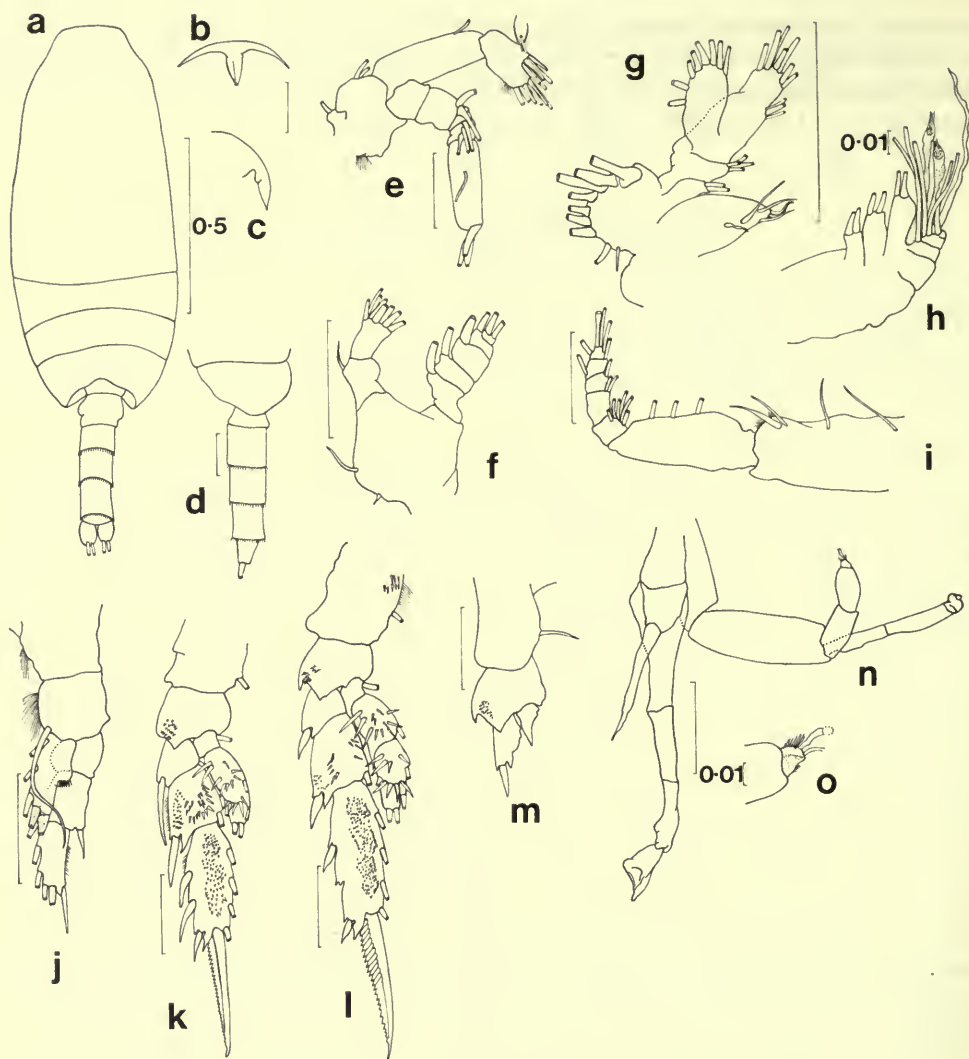


FIG. 17. *Amallothrix lobophora* ♂. a, body, dorsal; b, rostrum, ventral; c, rostrum, lateral; d, last thoracic segment and abdomen, lateral; e, 2nd antenna; f, mandibular palp; g, 1st maxilla; h, 2nd maxilla, lobes 4 and 5 omitted; i, maxilliped; j, 1st leg; k, 2nd leg; l, 3rd leg; m, 4th leg; n, 5th leg; o, 5th leg, last exopodite segment left leg. Bar scale 0.1 mm unless indicated.

Amallothrix altera (Farran, 1929)

Amallophora altera Farran, 1929 : 252-4, fig. 19; Tanaka, 1960 : 102.

Scolecithricella sp. 1 (part) Roe, 1972a : 304, 310; 1972c : 540.

? *S. (Amallothrix) altera*; Vervoort, 1965 : 69-73, figs 14-16.

? *S. (Amallothrix) auropecten*; Vervoort, 1951 : 101-3, fig. 54.

not *Amallophora altera*; Vervoort, 1957 : 94-95, figs 77-79; Bradford, 1973 : 134, 136, 141, 144-5, figs 2-3.

MATERIAL EXAMINED: 1 female from an N113H haul fished at 700–550 m depth off Fuerteventura (28°N 14°W) on 24 November 1963. 3 females from 2 RMT 1 hauls fished at 600–410 m depth in a position 18°N 25°W on 15 and 16 November 1969. Deposited at the British Museum (Natural History), reg. no. 1974 : 616–619.

DESCRIPTION. Female (Fig. 18): Body length 1.98–2.20 mm with a mean of 2.09 mm (4 specimens). The cephalothorax is 4.1 times as long as the 4-segmented abdomen. The head and 1st thoracic segment are fused; thoracic segments 4 and 5 are separate. The rostrum is large and has two filaments which are thickened

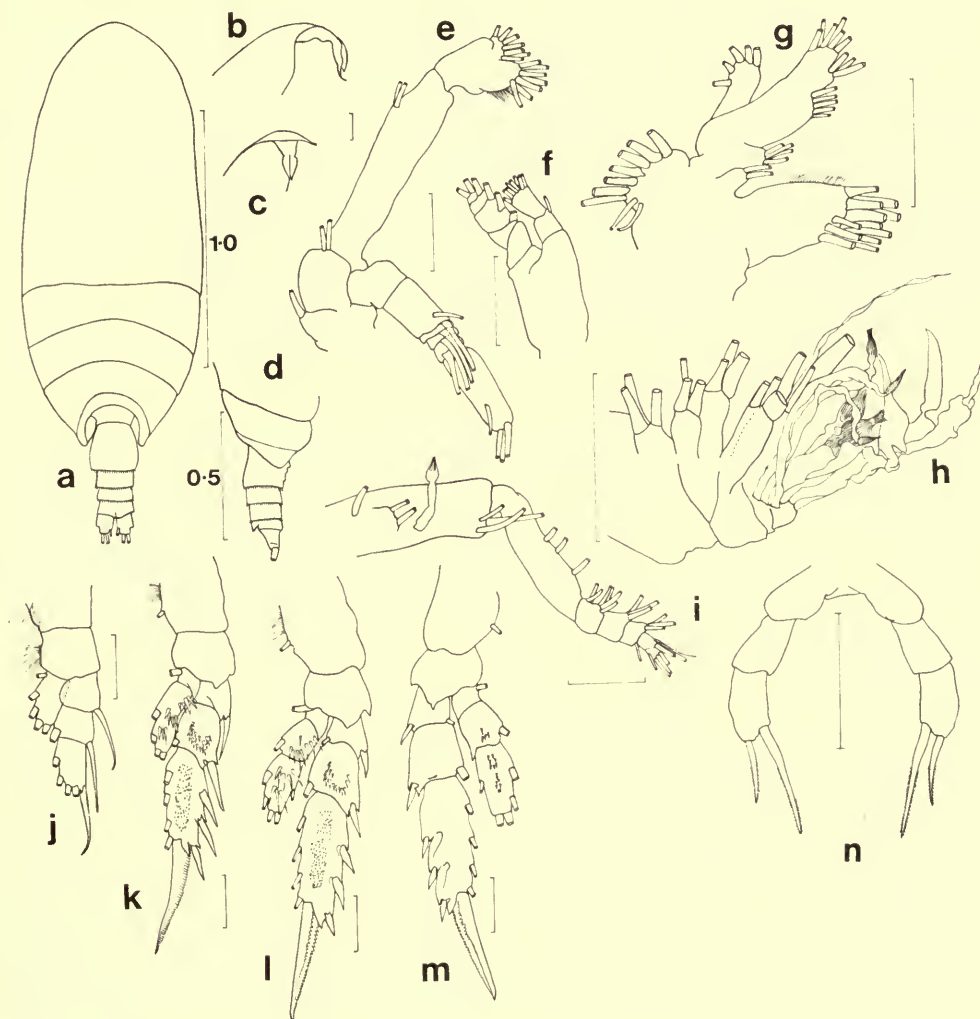


FIG. 18. *Amallothrix altera* ♀. a, body, dorsal; b, rostrum, half lateral; c, rostrum, ventral; d, last thoracic segment and abdomen, lateral; e, 2nd antenna; f, mandibular palp; g, 1st maxilla; h, 2nd maxilla; i, maxilliped; j, 1st leg; k, 2nd leg; l, 3rd leg; m, 4th leg; n, 5th leg. Bar scale 0.1 mm unless indicated.

basally. The last thoracic segment protrudes laterally. The genital segment is slightly longer than the combined length of the three subsequent segments. The furcal rami are about $1\frac{1}{4}$ times as long as wide. The 1st antenna has 24 segments (the last is very small), and reaches to the hind edge of the genital segment. The remaining mouthparts are as shown. The endopodite of the 2nd maxilla has five brush-like setae, of which two are enlarged, and three flattened worm-like setae. The maxilliped has a large brush-like seta on the 1st basipodite. The legs are as shown. The endopodite of the 1st leg has no lobe and no surface spines. The 5th leg has three segments on each side.

REMARKS. The present females have been compared with the type specimens of *Amallophora altera* held in the collections of the British Museum (Natural History). They are smaller than Farran's types but are structurally identical except that the holotype has two setae on the basipodite of the mandibular palp and no apparent segmentation line between endopodite segments 4 and 5 of the maxilliped. Farran (1929) could not ascertain the structure of the sensory setae of the 2nd maxilla. However, both holotype and paratype are identical to the females described here and have two large brush-like setae and three smaller ones. There is no doubt that the present females are conspecific with *Amallophora altera* Farran.

The identity of this species is confused and it has been mixed up with *Amallothrix auropecten* (Giesbrecht, 1892). For comparison the latter species is described below (p. 333). Bradford (1973) described as *Amallophora altera* a species having one very large and four small brush-like setae on its 2nd maxilla. This arrangement is conspicuously different from both the present material and Farran's types. Bradford's specimen is incompletely described but it also differs from *Amallothrix altera* in the structure of its rostrum, its 1st maxilla and in its 1st and 5th legs. It is clearly a different species. Bradford used her specimen to typify a group containing *Amallophora smithae* Grice, 1962, *Scolecithrix vorax* Esterley, 1911 and *Xanthocalanus typicus* Farran, 1908. This group of species is considered here to comprise a new genus which is described later on p. 335. The true *Amallothrix altera* does not belong in this new genus.

Vervoort's (1957) description is also incomplete but his specimens differ from the present species by (a) a short outer edge spine on the 1st exopodite segment of the 2nd leg, (b) an incompletely segmented 5th leg, (c) differences in the setation of the 1st maxilla and (d) apparent differences in the endopodite of the 2nd maxilla, although the description is not very clear on this. These specimens may be *A. auropecten* but their identification cannot be certain from his description. Similarly the definite identity of his 1951 specimen cannot be determined. It has a 3-segmented 5th leg but Vervoort (1957) stated that it was conspecific with his later material. In 1965 Vervoort described a further specimen which may be *Amallothrix altera*, but the rostrum appears to be smaller and the endopod of the 2nd maxilla is different, although this may be due to the difficulty in seeing the small brush-like heads.

A. altera is generally similar to *A. auropecten* (Fig. 19) but differs in the following respects, (a) the rostrum of *A. altera* is larger and of a different shape, (b) the setation of the 1st maxilla is different, especially of the exopodite, (c) the endopodite of the

2nd maxilla has two of the five brush-like setae enlarged in *A. altera* but not in *A. auropecten*, (d) the 1st basipodite of the maxilliped has a large brush-like seta in *A. altera* but not in *A. auropecten*, (e) the endopod of the 1st leg has a comb of surface spines in *A. auropecten* but not in *A. altera*, and (f) the 5th leg has three segments in *A. altera* but is incompletely segmented in *A. auropecten*. This last difference may be variable but all the examined specimens of *A. altera* have a completely segmented 5th pair of legs whereas those of *A. auropecten* are normally 2-segmented or incompletely divided into three (Fig. 19 and see Giesbrecht, 1892; Rose, 1942; Wilson, 1942, 1950; Park, 1968; Bradford, 1973). One of the present specimens of *A. auropecten* has an abnormal 5th pair of legs similar to that figured by Park (1968, pl. 9, fig. 3).

In 1965 Vervoort transferred Farran's *Amalophora altera* to *Amallothrix*. The main apparent difference between the species and Bradford's redefinition of *Amallothrix* is its *Scaphocalanus*-type 1st maxilla with three surface setae on the 1st inner lobe. This character is shared with *A. lobophora* (p. 329) and *A. auropecten* (p. 334) and discussion of the affinities of all three species follows on p. 334. The enlargement of two of the brush-like setae in the present species is not, by itself, a generic character and it is shown by several other species and genera within the Scolecithricidae (see, for example, *A. falcifer*, p. 325, *Scolecithricella obscura*, p. 318, *Scaphocalanus difficilis*, p. 315, and *Scopalatum dubia*, p. 338).

Amallothrix auropecten (Giesbrecht, 1892)

Scolecithrix auropecten Giesbrecht, 1892 : 266, pl. 13, figs 8, 18, 22, 27, pl. 37, figs 3, 10.

Scolecithricella auropecten; Rose, 1933 : 158-9, fig. 175.

S. sp. 1 (part) Roe, 1972a : 296, 304, 310; 1972c : 540.

? *Amalophora altera*; Vervoort, 1957 : 94-5, figs 77-79.

? not *Scolecithricella* (*Amallothrix*) *auropecten*; Vervoort, 1951 : 101-3, fig. 54.

MATERIAL EXAMINED : 2 females and 21 males taken in 11 N113H hauls made at 950-475 m depth off Fuerteventura (28°N 14°W), between 24 and 28 November 1965. 6 females and 6 males taken in 7 RMT 1 hauls made at 785-300 m depth in a position 18°N 25°W, between 13 and 16 November 1969.

DESCRIPTION (Fig. 19) : Body length of the females is 1.9-2.05 mm with a mean of 1.96 mm (7 specimens); of the males it is 2.20-2.51 mm with a mean of 2.28 mm (21 specimens). The present females agree with the descriptions of Giesbrecht (1892) and Rose (1942). They are figured here for comparison with *A. altera* (p. 330) where their structure is commented upon. The endopod of the 2nd maxilla has five brush-like setae, all with small heads, but only four could be seen in the specimen illustrated. The males agree with Rose's account and redescription is unnecessary. The male described by Wilson (1950) as *Scolecithricella auropecten* is not of this species.

REMARKS. Rose (1942) transferred *Scolecithrix auropecten* to *Amallothrix*. Bradford (1973) omitted it from her redefined *Amallothrix* and considered that it should typify an unnamed group, together with *Scolecithrix laminata* Farran, 1926

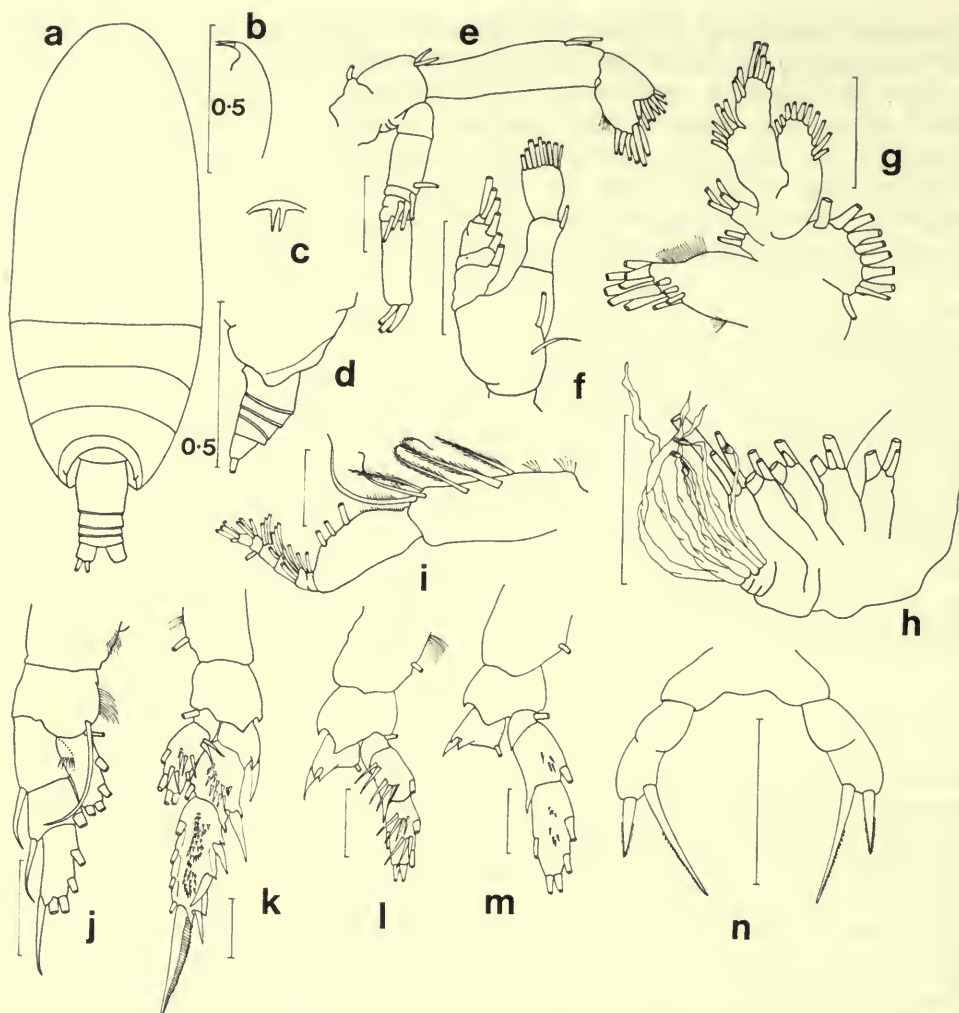


FIG. 19. *Amallothrix auropecten* ♀. a, body, dorsal; b, rostrum, lateral; c, rostrum, ventral; d, last thoracic segment and abdomen, lateral; e, 2nd antenna; f, mandibular palp; g, 1st maxilla; h, 2nd maxilla; i, maxilliped; j, 1st leg; k, 2nd leg; l, 3rd leg; m, 4th leg; n, 5th leg. Bar scale 0.1 mm unless indicated.

and *Scolecithricella modica* Tanaka, 1962. *Scolecithrix* (= *Scolecithricella*) *laminata* differs in many respects from the present species (see p. 320) and is not, in my opinion, closely related. *A. altera* and *A. lobophora*, however, do seem to be related to the present species. All three differ from Bradford's *Amallothrix* in having a *Scaphocalanus*-type 1st maxilla (p. 329). The female 5th legs of all three species and the male 5th legs of *A. lobophora* and *A. auropecten* are also atypical of this genus. There are, however, differences between these three species. *A. altera* and *A. auropecten* are distinct (p. 332), and *A. lobophora* differs from both by lacking an

outer edge spine on the 1st exopodite segment of the 1st leg and by having spines on the 1st basipodite of the 3rd leg. The rostrum of *A. lobophora* is similar to that of *A. altera* but the structure of its 5th legs (both sexes), the spiny lobe on the endopod of the 1st leg, and the uniformly small brush-like setae on the female 2nd maxilla are all more like *A. auropecten*. Whether or not these three species are sufficiently alike and sufficiently distinct from others to stand as a separate genus within the Scolecithricidae is not yet clear. Discovery of the male of *A. altera* and determination of the acceptable generic limits, especially regarding the 1st maxilla, will clarify their position. Meanwhile all three species can conveniently remain within *Amallothrix*.

SCOPALATUM gen. nov.

DIAGNOSIS. *Head* and 1st thoracic segment fused; thoracic segments 4 and 5 fused or separate. *Rostrum* with two filaments. *1st antenna* with 23 segments in the female, 20 in the male; there are large sensory filaments on the proximal segments of the male 1st antenna. *2nd antenna* exopod slightly longer than the endopod. *1st maxilla* with two posterior surface setae on the 1st inner lobe, two setae on the 2nd inner lobe and four on the 3rd inner lobe; in the female the endopod is ornamented with spinules. *2nd maxilla* endopod with five brush-like setae and three flattened worm-like setae; in the female one of the brush-like setae is greatly enlarged; in the male two are enlarged. *Maxilliped* with one brush-like seta on the 1st basipodite. The male mouthparts are weakly chitinized and slightly reduced.

1st leg has a 3-segmented exopod and a single endopodite segment: all three exopodite segments have an outer spine; the endopod has a lobe carrying small spines. *2nd leg* has a 3-segmented exopod and a 2-segmented endopod; the outer edge spines on all exopodite segments are large; the 2nd and 3rd exopodite segments and the 2nd endopodite segment carry prominent surface spines. *3rd leg* has a 3-segmented exopodite and endopodite: the 1st basipodite segment has a group of long spines; the 2nd and 3rd exopodite and endopodite segments have surface spines. *4th leg* has a 3-segmented exopodite and endopodite: the 1st basipodite may have a group of long spines; the 2nd and 3rd endopodite segments have very few small surface spines; the exopodite segments have no surface spines. *Female 5th leg* is uniramous; on each side there are two segments, which may be fused, attached to a common basal segment; there are 1–3 spines. *Male 5th leg* similar to that of *Scaphocalanus*: left exopod is shorter than the endopod; right exopod is much longer than the endopod.

Scopalatum gibbera sp. nov. is nominated as the type species of the genus.

The name *Scopalatum* is derived from the Latin *scopae* – a broom and *latum* – carried; it refers to the sensory setae of the 2nd maxilla.

DISCUSSION. T. Scott (1894) described a new subgenus, *Amallophora*, for a male copepod, *A. typica*, having a peculiar enlarged sensory seta on its 2nd maxilla. Giesbrecht (1892) had previously described a similar structure in the male of *Xanthocalanus* and considered that *Amallophora* was a junior synonym of *Xanthocalanus* (Giesbrecht & Schmeil, 1898). Farran (1908) named a female which he believed to be conspecific with Scott's male as *X. typicus*. Recently, Bradford

(1973) separated these two specimens, reiterating Giesbrecht's opinion that Scott's male is a xanthocalanid but transferring Farran's female to the Scolecithricidae. She placed this, as *X. typicus* Farran, into a group together with *Amallophora smithae* Grice, 1962, *Scolecithrix vorax* Esterley, 1911 and *Amallophora altera* Farran, 1929. Her inclusion of *A. altera* in this group however is erroneous, see p. 332; Bradford's specimen of *A. altera* is not conspecific with Farran's, which belongs to an entirely different group. Nevertheless, I believe she was correct in collecting together her specimen of '*A. altera*' and the other three species into a distinct group within the Scolecithricidae.

Bradford briefly characterized this group but did not name it as a separate genus. The discovery of a female of a new species which clearly belongs in this group (see below) and the redescription of what, in my opinion, is a male of this group (p. 338) lead me to believe that this collection of species should be given generic status within the Scolecithricidae. This new genus is defined above (p. 335). The genus *Scopalatum* at present contains *S. farrani* sp. nov., *S. vorax* (Esterley, 1911), *S. smithae* (Grice, 1962), *S. dubia* (T. Scott, 1894) and *S. gibbera* sp. nov. It also includes the species '*Amallophora altera*' wrongly identified by Bradford (1973) which should be further described and named. Grice's (1962) account of *S. smithae* is complete and also conforms with the new genus. The descriptions of *S. vorax* (Esterley, 1911) and '*A. altera*' of Bradford (1973) are incomplete, however, particularly regarding the swimming legs. The present generic definition may have to be modified when these latter two species are fully described. Details of *S. gibbera* sp. nov., *S. farrani* sp. nov. and *S. dubia* (T. Scott, 1894) are given below.

Scopalatum agrees in all respects with Bradford's (1973) redefinition of the Scolecithricidae. The combination of characters given on p. 335, especially those of the 1st and 2nd maxillae and the legs, distinguishes this new genus from all others in the family. It is related to *A. altera*, *A. auropecten* and *A. lobophora*, see p. 334. These three species may have to be removed from *Amallothrix* but they differ from the present genus in the structure of their 1st maxilla and, in the females, of the 2nd maxilla. The 2nd maxilla of the male *A. auropecten* is also distinct, and both this species and *A. altera* are further distinguished by having no basipodite spines on either their 3rd or 4th legs. *A. lobophora* has a similar 2nd maxilla in the male to *Scopalatum* and both sexes have a group of spines on the 1st basipodite of the 3rd leg. They do not, however, have an external spine on all exopodite segments of the 1st leg.

Scopalatum gibbera sp. nov.

Amallophora sp. Roe, 1972a : 295, 309.

MATERIAL EXAMINED : 1 female in an N113H haul fished at 310–240 m depth off Fuerteventura (28°N 14°W) on 13 November 1965. 2 females in 2 RMT 1 hauls fished in a position 18°N 25°W; one (the holotype) caught at 300–210 m depth on 12 November 1969 and the other at 400–305 m depth on 17 November 1969. Deposited at the British Museum (Natural History), holotype reg. no. 1974 : 620, paratypes reg. no. 1974 : 621–622.

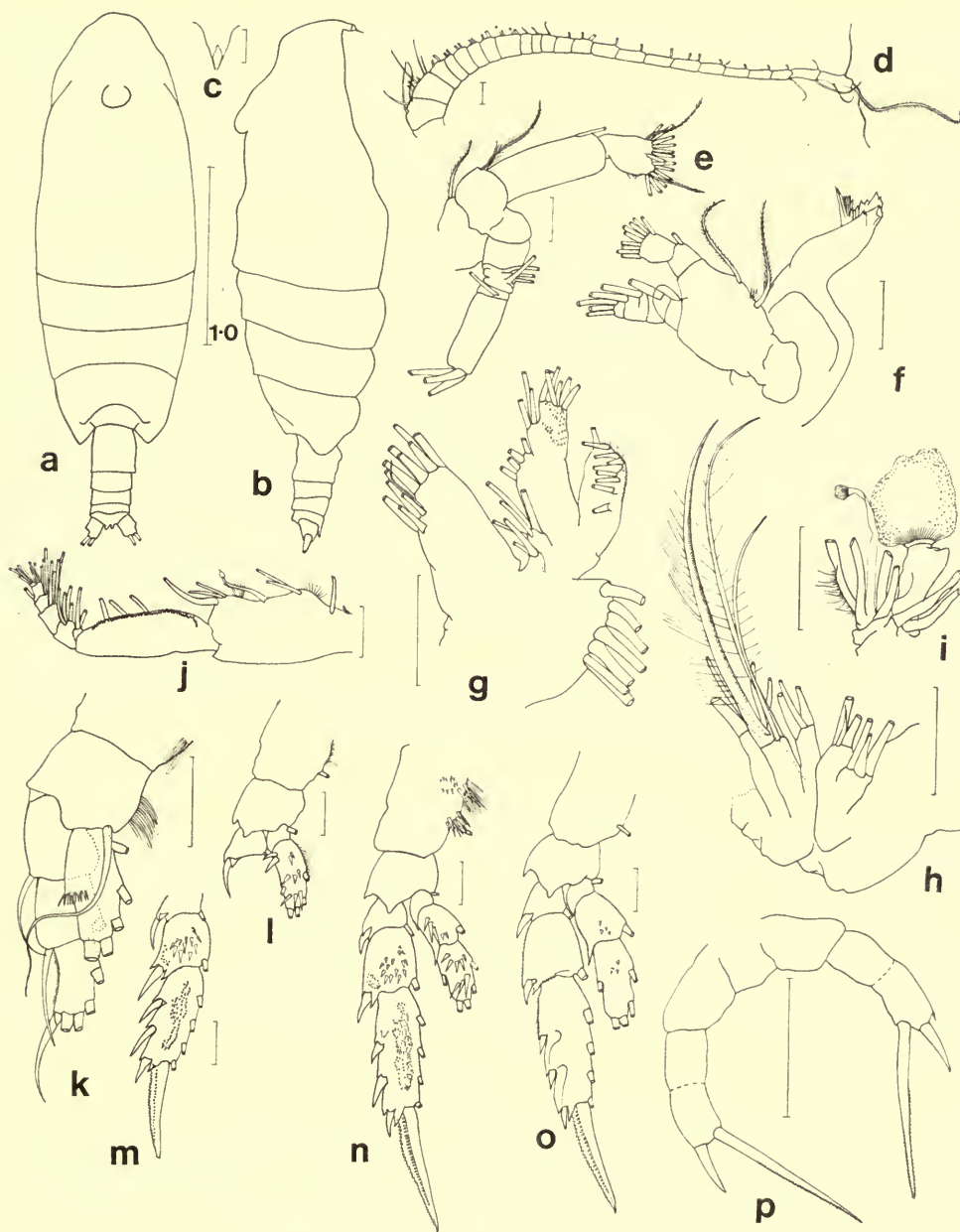


FIG. 20. *Scopalatium gibbera* ♀. a, body, dorsal; b, body, lateral; c, rostrum, ventral; d, 1st antenna; e, 2nd antenna; f, mandible; g, 1st maxilla; h, 2nd maxilla, exopod; i, 2nd maxilla, endopod; j, maxilliped; k, 1st leg; l, 2nd leg; m, 2nd leg, exopodite segments 2-3 (paratype); n, 3rd leg; o, 4th leg; p, 5th leg. Bar scale 0.1 mm unless indicated.

DESCRIPTION. Female (Fig. 20): Body length 2.58–2.81 mm with a mean of 2.73 mm (3 specimens). The holotype measures 2.81 mm. The cephalothorax is robust and 3.9 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are fused, as are thoracic segments 4 and 5. The mid-dorsal region of the head has a very characteristic protuberance which is particularly conspicuous when seen from the side. The rostrum has two filaments with thickened bases. The hind margin of the cephalothorax is deeply indented laterally. The genital segment has a slight ventral protrusion and is longer than the combined length of the three following segments. The furcal rami are about as long as wide. The 1st antenna has 23 segments and does not quite reach the end of the cephalothorax. The remaining mouthparts and the legs are as shown. The endopod of the 1st maxilla is covered with small spines. The endopodite of the 2nd maxilla has five brush-like and three flattened worm-like setae, one of the brush-like setae is greatly enlarged. The 1st basipodite of the maxilliped has one brush-like seta. The 1st basipodite of the 3rd leg has two conspicuous groups of long spines. The terminal spines on legs 2–4 have laminae. The 5th pair of legs is uniramous with two fused segments on each side attached to a basal segment; the line of fusion is clearly visible. The terminal segment on each side has one long and one shorter spine. There is an additional small spine on one side only, but this is clearly variable since in one of the paratypes it is about halfway down the outside edge of the fused 2nd and 3rd segments.

REMARKS. *S. gibbera* has all the female characters defined for the genus on p. 335. A discussion of its affinities has been given earlier.

Scopalatum farrani sp. nov.

Xanthocalanus typicus; Farran, 1908: 47–48, pl. 4, figs 15–17; Bradford, 1973: 145.

Amallophora typica; Sars, 1924: pl. 38, figs 8–18; 1925: 140–142 (part); Rose, 1933: 134–135 (part), fig. 129; Wilson, 1942: 170–171, fig. 1; Wilson, 1950: 159 (part), pl. 20, fig. 275; Vervoort, 1957: 94–95 (part); Tanaka, 1960: 102 (part); Vervoort, 1965: 27–28 (part); Binet & Dessier, 1971: 430, 453; Bradford, 1973: 138–139 (part).

? *Amallophora typica*; Grice & Hulsemann 1965: 221, 223; Harding, 1972: 58.

not *Xanthocalanus typicus*; Giesbrecht, 1897: 254; Giesbrecht & Schmeil, 1898: 50; Wolfenden, 1908: 35.

not *Amallophora typica* T. Scott, 1894: 54, pl. 3, figs 39–46, pl. 6, figs 1–4; A. Scott, 1909: 85, pl. 36, figs 1–8.

The female described by Farran (1908) as *X. typicus* was misidentified and belongs to a new species which I have named *Scopalatum farrani*. The female specimens of *S. farrani* in the collections of the Institute of Oceanographic Sciences agree completely with the generic definition of *Scopalatum* given earlier.

Scopalatum dubia (T. Scott, 1894)

Amallophora dubia T. Scott, 1894: 55, pl. 4, figs 10–18.

Scolecithrix scotti Giesbrecht, 1897: 254; Giesbrecht & Schmeil, 1898: 46; Wolfenden, 1911: 250.

Heteramallia dubia; Sars, 1907: 17 (part); A. Scott, 1909: 86–87 (part); Sars, 1925: 142–144 (part); Rose, 1933: 135 (part); Alzamora, 1940: 6; Wilson, 1942: 189 (part); Vervoort, 1965: 28–30 (part).

Heteremallia dubia; Rose, 1929: 26.

Hetermalla dubia; Roe, 1972a: 303, 309.

? *Heteramallia dubia*; Wilson, 1950: 239; Grice & Hulsemann, 1967: 16.

not *Heteramallia dubia*; A. Scott, 1909: pl. 33, figs 1–9; Sars, 1924: pl. 39; Rose, 1933: fig. 130; Grice & Hulsemann, 1965: 221, 223, 235.

MATERIAL EXAMINED: 1 male in an N113H haul made at 660–510 m depth off Fuerteventura (28°N 14°W) on 26 November 1965. 8 males taken in 5 RMT 1 hauls made at 900–305 m depth in a position 18°N 25°W between 12 and 17 November 1969. 7 males deposited at the British Museum (Natural History), reg. no. 1974: 623–629.

DESCRIPTION. Male (Fig. 21): Body length 2.36–2.74 mm with a mean of 2.48 mm (9 specimens). The cephalothorax is 2.7 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are fused; thoracic segments 4 and 5 are separate. The rostrum has two filaments attached to a common base. The hind margin of the cephalothorax has a slight lateral indentation. The 1st antenna reaches to the hind edge of the 2nd abdominal segment; both 1st antennae have 20 segments and the proximal 12 segments on each side carry large flattened sensory filaments. The mouthparts and legs are as shown. The endopod of the 2nd maxilla has five brush-like setae and three flattened worm-like setae; the heads of three of the brush-like setae are small whereas two are greatly enlarged – one of them especially so. All the 'brush' heads consist of fine threads ending in rounded swellings. The 1st basipodite of the 3rd leg has two groups of long narrow spines. The 5th pair of legs is similar to that of *Scaphocalanus* and reaches back to the end of the furcal rami. On the right leg the exopodite terminates in a claw-like segment. On the left leg the exopodite is shorter than the endopodite; the 3rd exopodite segment is covered with hairs and has a terminal lamella.

REMARKS. I have compared the present males with the type specimens of *Amalophora dubia* T. Scott, 1894 held in the collections of the British Museum (Natural History). The type material consists of several slides on which are mounted the mixed appendages and abdomens of two specimens. There is only one example of most appendages – including the 2nd maxilla, and there is no specimen of the 1st maxilla. Neither of the two cephalosomes is in the Museum's collection. The material is very faded and it is impossible to ascertain the detailed structure of some of the appendages. An attempt to remount some of the specimens failed because the mountant would not dissolve. The only observable difference between the present males and Scott's type is in the 3rd leg where the type does not, apparently, have spines on the 1st basipodite. This limb is figured by Scott but wrongly described as the 4th leg (Scott, 1894: Pl. 4, fig. 16). According to Scott the right 1st antenna has 18 joints and is indistinctly geniculate and the left 1st antenna has 23 joints. There are three 1st antennae in the type collection; one has 19 segments but the others are very faded and have, I believe, 20 and 21 segments respectively. None of these antennae are in any way geniculate and their segmentation agrees

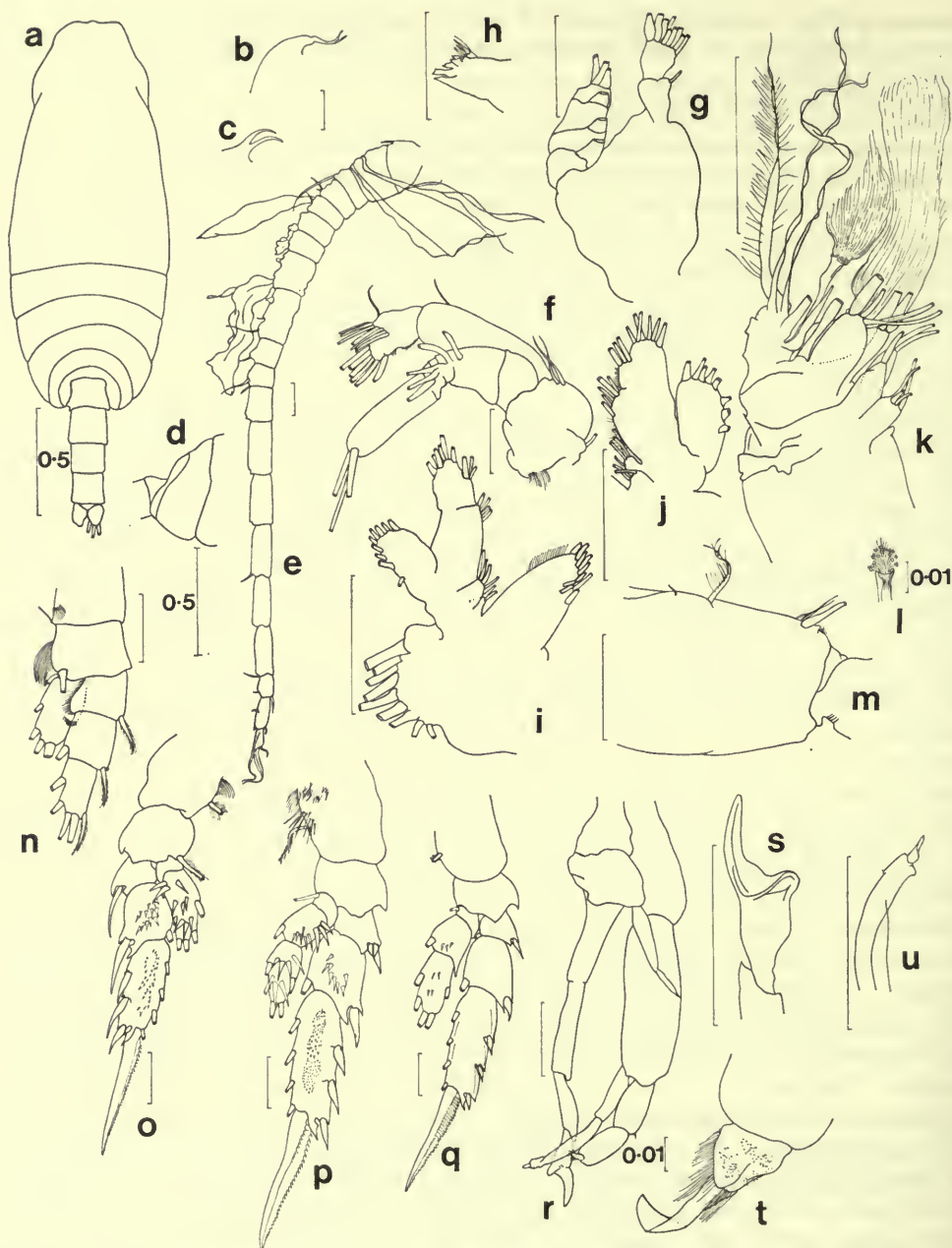


FIG. 21. *Scopalatum dubia* ♂. a, body, dorsal; b, rostrum and forehead, lateral; c, rostrum, ventral; d, last thoracic segment, lateral; e, 1st antenna; f, 2nd antenna; g, mandibular palp; h, mandible blade; i, 1st maxilla; j, 1st maxilla (different specimen); k, 2nd maxilla; l, 2nd maxilla, head of small brush-like seta; m, maxilliped, basal segment (different specimen); n, 1st leg; o, 2nd leg; p, 3rd leg; q, 4th leg; r, 5th leg; s, 5th leg, last exopodite segment right leg; t, 5th leg, last exopodite segment left leg; u, 5th leg, last endopodite segment left leg (different specimen). Bar scale 0.1 mm unless indicated.

better with the present male's antennae, which have 20 segments on each side, than with Scott's description. The type material of the 2nd maxilla is in very poor condition and it is impossible to see any structure except the general presence of two large brush-like setae. Despite the possible difference in the 3rd leg I believe that the present males are conspecific with Scott's *Amallophora dubia*.

Sars (1907) erected a genus, *Heteramalla*, for a female which he believed was conspecific with Scott's male. In 1925, however, he expressed doubts as to the correctness of his assumption, and in 1965 Vervoort also mentioned the possibility that Sars' females and Scott's male were not the same species. Further male specimens have been recorded by Wolfenden (1911) and by Rose (1929) but they were not described.

Bradford (1973) transferred *Heteramalla* from the Phaennidae to the Scolecithridae. The present males are clearly scolecithricids according to her redefinition of the family. I have examined female specimens of *H. dubia* Sars, 1907 taken at 1020–800 m depth in a position 18°N 25°W. These specimens agree with Sars' (1924, 1925) description except that they have no 5th pair of legs (thereby conforming with Grice & Hulsemann's (1965) specimen), and there is no seta on the 2nd inner lobe of the 1st maxilla. The endopod of the 3rd leg has two segments only. These females also agree with Bradford's definition of the Scolecithricidae. I believe, however, that Sars was mistaken in identifying his female with Scott's male. Apart from the normal sexual differences they differ in the following respects: (a) the rostrum of ♀ *H. dubia* is strong and plate-like, in the male it has two filaments, (b) the 1st maxilla of the males has two setae on the surface of the 1st inner lobe, two on the 2nd inner lobe and four on the 3rd inner lobe; the corresponding number of setae in the female are 1, 0 and 3, (c) the 1st leg of ♀ *H. dubia* has a 2-segmented exopod with no external spine on the 1st exopodite segment; the endopod has no lobe and has a group of large spines; in the male the 1st leg has three exopodite segments, all with outer spines, and the endopod has a lobe with a comb of small spines only, (d) ♀ *H. dubia* has no surface spines on the exopodites of legs 2–4—these legs are heavily spinulated in the male, and (e) the 3rd leg of the ♀ *H. dubia* has a 2-segmented endopod and has no spines on the 1st basipodite segment; the 3rd leg of the male has three endopodite segments and two groups of spines on the 1st basipodite.

I agree with Bradford (1973) that the genus *Heteramalla* Sars, 1907 belongs to the Scolecithricidae. It is at present a monospecific genus known only from the female (see p. 342). Scott's male is here considered to belong to the new genus *Scopalatum* described on p. 335.

The most striking difference between *S. dubia* and the females of *Scopalatum* is in the development of the sensory setae of the 2nd maxilla. The females have one brush-like seta much enlarged but the male has two. Enlargement of one or two of these setae is, however, common to the males of many species and genera of the Scolecithricidae (see, for example, *Amallothrix falcifer*, p. 325, and *Scolecithricella dentata* (Rose, 1942: 55). I believe that the increased size of one seta in the present males is a sexual character. Apart from the normal sexual differences in the 1st antenna and more weakly chitinized and slightly reduced mouthparts, the

appendages of these males are very similar to those of the female *S. gibbera* sp. nov., *S. farrani* sp. nov. and *S. smithae* Grice, 1962. They are so similar to *S. gibbera* that these two species may be conspecific. They differ in the length of the outer edge spines of the exopodite of the 1st leg, and the males do not have the curious dorsal swelling of the female. In addition to these differences *S. farrani* has groups of spines on the 1st basipodite of the 4th leg. *S. smithae* and *S. vorax* are much smaller species.

***Heteramalla sarsi* sp. nov.**

Heteramalla dubia; Sars, 1907: 17 (part); A. Scott, 1909: 86–87 (part), pl. 33, figs 1–9; Sars, 1924: pl. 39; 1925: 142–144 (part); Rose, 1933: 135 (part) fig. 130; Wilson, 1942: 189 (part); Grice & Hulsemann, 1965: 221, 223, 235; Vervoort, 1965: 28–30 (part).
? *Heteramalla dubia*; Wilson, 1950: 239; Grice & Hulsemann, 1967: 16.
not *Heteramalla dubia*: Alzamora, 1940: 6.

The female described by Sars (1907) as *H. dubia* was misidentified and belongs to a new species which I have named *H. sarsi*. The validity of this species is considered earlier together with the discussion of *Scopalatum dubia* (T. Scott).

Family **METRIDIIDAE**

***Metridia alata* sp. nov.**

MATERIAL EXAMINED: 6 females and 6 males taken in 6 RMT 1 hauls made at 1220–700 m depth in a position 18°N 25°W, between 12 and 18 November 1969. The holotype (female) and allotype (male) were caught on 18 November 1969 at 1220–1000 m. Deposited at the British Museum (Natural History), holotype reg. no. 1974: 630, paratypes reg. no. 1974: 631–641.

DESCRIPTION. Female (Fig. 22): Body length 8.64–10.24 mm with a mean of 9.09 mm (5 specimens). The holotype measures 9.12 mm. The cephalothorax is 1.2 times as long as the 3-segmented abdomen. It is very robust and in lateral view the anterior part of the head protrudes sharply from the hind part. The right lateral margin of the head is produced into a very conspicuous wing; this wing protrudes both laterally and ventrally and is present on the right side only. The head and 1st thoracic segment are separate; thoracic segments 4 and 5 are fused. The rostrum has two strong spikes pointing ventrally. The hind edge of the cephalothorax is smooth and rather abruptly rounded. The genital segment is swollen both laterally and ventrally and is longer than the combined length of the two subsequent segments. The furcal rami are 0.36 times the length of the abdomen and are 6 times longer than wide. The 1st antenna is slightly longer than the body: it has 25 segments, segments 7 and 8 are partially fused and the last segment is small; the 1st segment has three hooks and the 2nd, 4th and 5th segments each have a single hook. The remaining mouthparts and legs are as shown. The endopodite of the mandibular palp has a group of large spines on the 1st segment and many small spines on the 2nd. The mandible blade has numerous small spines in addition to the large teeth. The

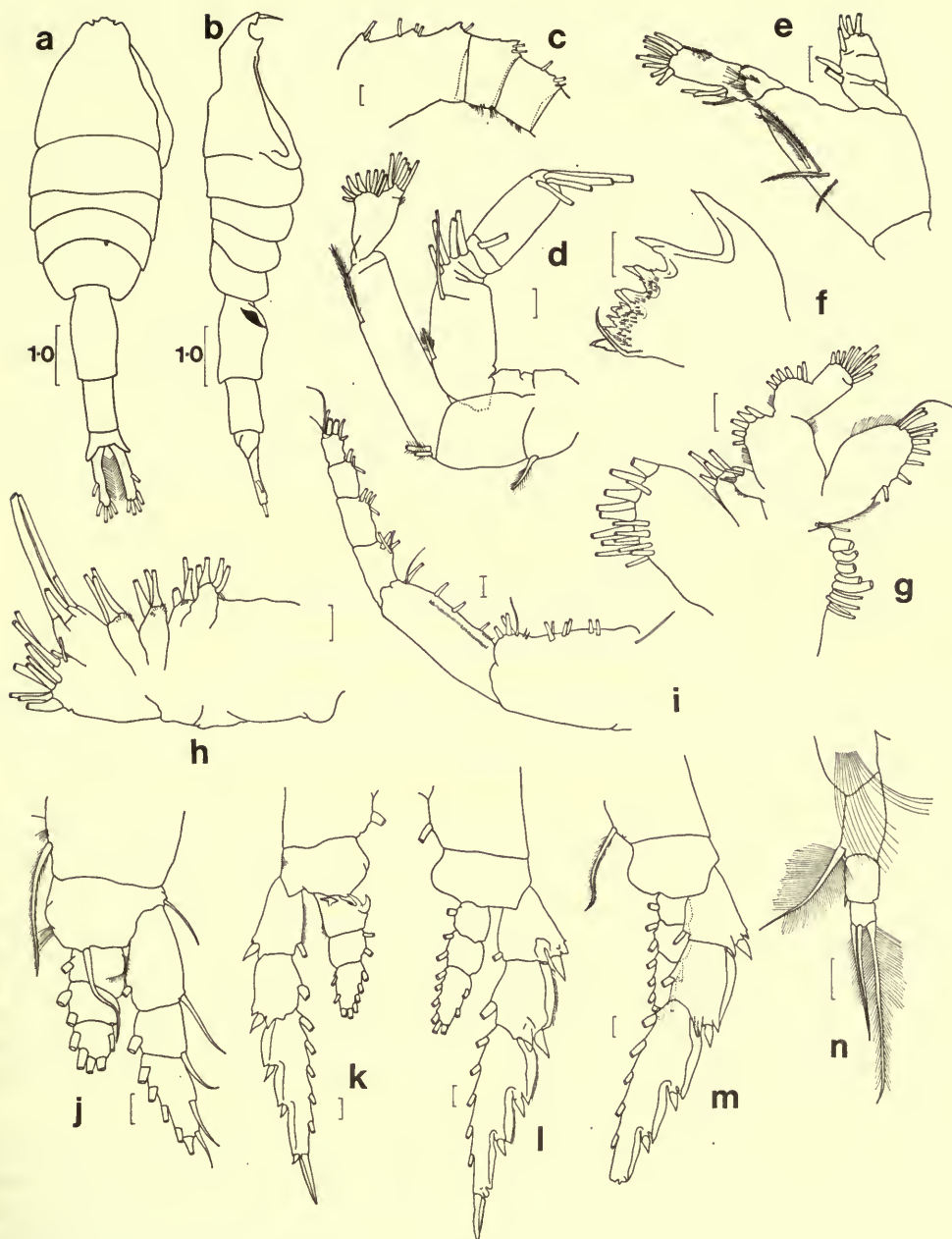


FIG. 22. *Metridia alata* ♀. a, body, dorsal; b, body, lateral; c, 1st antenna, basal segments; d, 2nd antenna; e, mandibular palp; f, mandible blade; g, 1st maxilla; h, 2nd maxilla; i, maxilliped; j, 1st leg; k, 2nd leg; l, 3rd leg; m, 4th leg; n, 5th leg. Bar scale 0.1 mm unless indicated.

1st endopodite segment of the 2nd leg has three strong claws. The 5th pair of legs is symmetrical; on each side the basipodite has a bunch of long hairs, the 1st segment has a plumose outer edge seta, the 2nd a short spine and the 3rd terminates with three plumose setae.

Male (Fig. 23a-b): Body length 8.00–8.64 mm with a mean of 8.51 mm (6 specimens). The allotype measures 8.64 mm. The appearance of the cephalothorax is as in the female; the head has a conspicuous wing on the right side only. The abdomen has five segments. The left 1st antenna is geniculate; both 1st antennae are slightly longer than the body. The remaining mouthparts and swimming legs are as in the female. The 5th pair of legs is asymmetrical: on the left side, the basal segment is longer than the right and has a bundle of hairs, the 4th segment terminates with two small spines; on the right side there are five segments, the 2nd bearing a long curved process and the 5th ending in three small spines.

REMARKS. The appendages of the present species are very similar to those of *Metridia princeps* Giesbrecht, 1892, but it can be distinguished easily from this and from all other species in the genus by the peculiar wing-like development of the right side of the head.

Family CENTROPAGIIDAE

Centropages caribbeanensis Park, 1970

MATERIAL EXAMINED: 43 females and 21 males from 6 RMT 1 hauls made at 194–0 m depth in a position 18°N 25°W, between 15 and 18 November 1969. 5 males are deposited at the British Museum (Natural History), reg. no. 1974: 642–646.

DESCRIPTION. Male (Fig. 23c-e): Body length 1.82–2.13 mm with a mean of 1.95 mm (15 specimens). The general appearance of the cephalothorax is as for the female; it is 2.2 times as long as the 5-segmented abdomen. The furcal rami are about 3 times longer than wide. The 1st antenna exceeds the body length by three or four segments. The right 1st antenna is geniculate and has 22 segments, segments 17, 18 and the proximal part of 19 have a row of fine teeth, the hinged joint is between segments 18 and 19. The remaining mouthparts and swimming legs are as in the female. The 5th pair of legs is asymmetrical. On the right side the terminal exopodite segment forms a large chela; on the left side the last exopodite segment has two large spine-like processes.

REMARKS. The present males were found in the same hauls as females which agree in every respect with Park's (1970) description. The male is similar to that of *C. elegans* Giesbrecht, 1895 described by Park (1968). It can be distinguished from this latter species by the 5th pair of legs. In *C. caribbeanensis* the spines on the terminal segment of the left exopodite are longer than in *C. elegans* and are not pitted distally. The shorter arm of the chelate right exopodite is pointed in *C. caribbeanensis* and rounded in *C. elegans*. The present specimens are only the second record of this species and the first from the eastern north Atlantic.

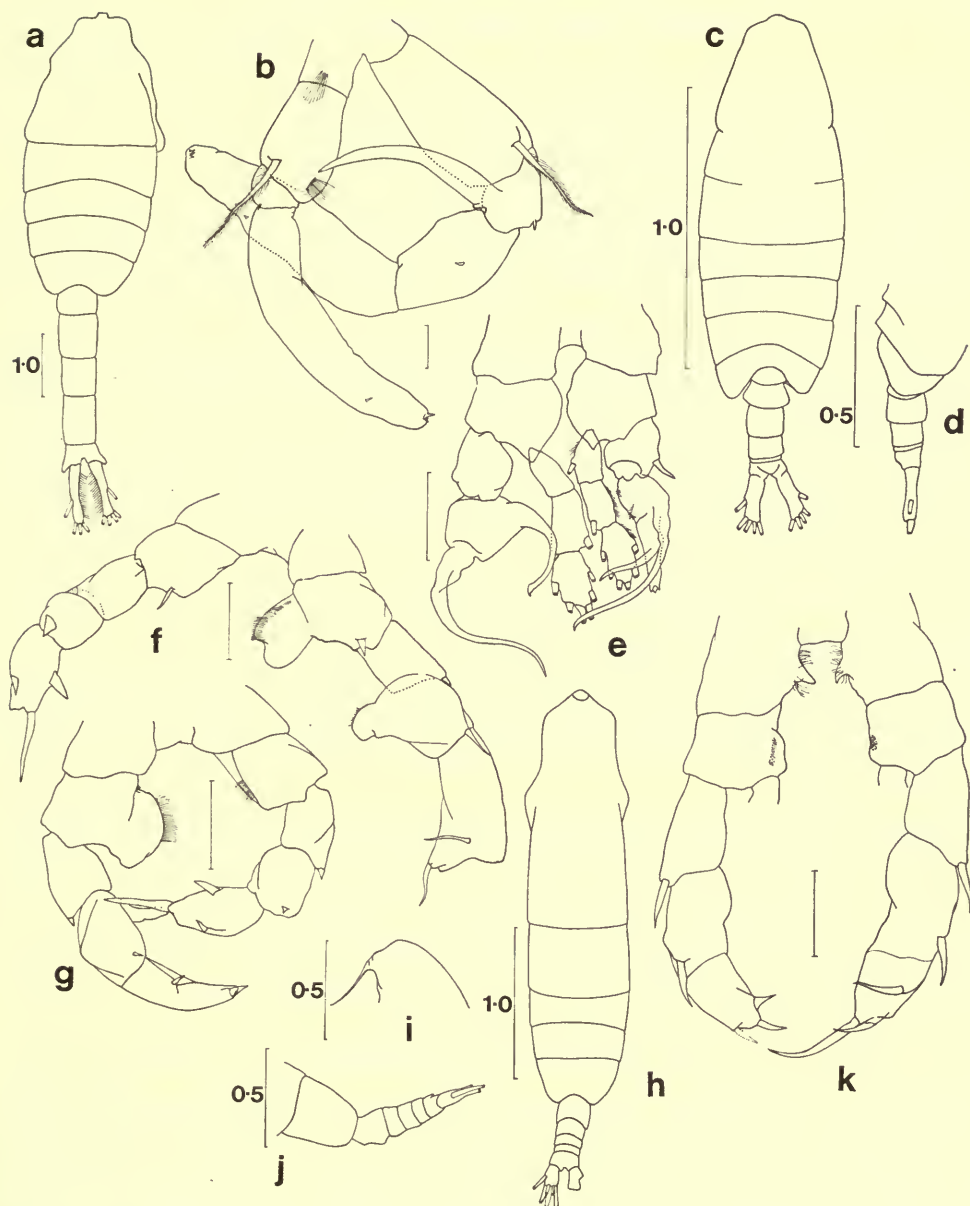


FIG. 23. a–b, *Metridia alata* ♂. a, body, dorsal; b, 5th leg. c–e, *Centropages caribbeanensis* ♂. c, body, dorsal; d, last thoracic segment and abdomen, lateral; e, 5th legs. f, *Heterorhabdus vipera* ♂ 5th legs. g, *Heterorhabdus tenuis* ♂ 5th legs. h–k, *Haloptilus angusticeps* ♂. h, body, dorsal; i, forehead and rostrum, lateral; j, last thoracic segment and abdomen, lateral; k, 5th legs. Bar scale 0.1 mm unless indicated.

Family **HETERORHABDIDAE***Heterorhabdus vipera* (Giesbrecht, 1892)

MATERIAL EXAMINED: 14 females and 4 males from 12 N113H hauls fished at 590–90 m depth off Fuerteventura (28°N 14°W), between 11 and 26 November 1965. 22 females and 3 males from 12 RMT 1 hauls made at 1250–110 m depth in a position 18°N 25°W between 12 and 17 November 1969.

REMARKS. The males of *H. vipera* and *H. tenuis* Tanaka, 1964 have been confused. Park (1970) described the male of *H. tenuis* as *H. vipera* (Roe, 1972*d*), and since the present material includes both species it seems advisable to illustrate the differences in their fifth pair of legs.

H. vipera (Fig. 23f) has a strongly asymmetric fifth pair of legs. The endopodites consist of three segments on both sides and have been omitted for clarity. The 3rd exopodite segment of the right leg is abruptly terminated and about as long as the combined length of the two previous segments. The present specimens differ slightly from that of Giesbrecht (1892) by having a spine on the 2nd basipodite segment of both legs, and by having an outer edge spine on the 2nd exopodite of the right leg. The similarity is such that I have no doubt that they are conspecific.

Heterorhabdus tenuis Tanaka, 1964

Heterorhabdus vipera; Park, 1970: 523–525, figs 250–252 (male only).

MATERIAL EXAMINED: 7 males from 5 N113H hauls made at 660–460 m depth off Fuerteventura (28°N 14°W), between 11 and 26 November 1965. 14 males from 6 RMT 1 hauls made at 600–210 m depth in a position 18°N 25°W, between 12 and 16 November 1969.

REMARKS. The present males agree with the descriptions of Tanaka (1964) and Park (1970 – as *H. vipera* ♂). The differences in the fifth pair of legs between *H. tenuis* and *H. vipera* can be seen clearly by comparing Figs 23g and 23f. In *H. tenuis* the 2nd basipodite of the left leg has a haired inner margin and the 3rd exopodite segment of the right leg is a totally different shape to that of *H. vipera*. Both endopodites have three segments and are omitted for clarity.

Family **AUGAPTILIDAE**

Several of the genera in this family, particularly *Euaugaptilus*, have recently been reviewed by Matthews (1972). Because of the high degree of intraspecific variation within this genus he used a system of numerical taxonomy, based upon 35 structural characters, to identify the various species. Tanaka & Omori (1974) also used a similar list of 21 characters to identify the *Euaugaptilus* spp. off Izu, Japan. These latter authors also recognized the great variation within species in this genus but retained a normal diagnostic key for their identification.

Several species of *Euaugaptilus* are described here, and all of them show marked intraspecific variations. This variability emphasizes the difficulties in recognizing or describing species based upon single specimens. Some *Euaugaptilus* species are

so similar to one another (see, for example, Matthews, 1972 : 66), that the discovery and description of more specimens is needed before firm conclusions can be reached regarding their validity.

Haloptilus angusticeps Sars, 1907

MATERIAL EXAMINED: 2 males and 7 females from 5 N113H hauls made at 625–0 m depth off Fuerteventura (28°N 14°W), between 17 and 26 November 1965. 12 females from 5 RMT 1 hauls made at 700–305 m depth in a position 18°N 25°W, between 14 and 17 November 1969. The males are deposited at the British Museum (Natural History), reg. no. 1974 : 647–648.

DESCRIPTION. Male (Fig. 23h–k): Body length 3.04–3.12 mm. The cephalothorax is long and slender and slightly more than 4 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are separate; thoracic segments 4 and 5 are fused. The rostral base is rounded and bears two fine fairly long filaments. The hind margin of the cephalothorax is smoothly rounded. The 1st antennae reach to the end of the furcal rami; the left 1st antenna is geniculate and has 20 segments, the hinge joint is in segment 18. The remaining mouthparts and swimming legs are similar to those of the female. The 5th pair of legs is slightly asymmetrical. On each side, the 1st basipodite segment has a pointed projection which is larger on the left, and the 2nd basipodite has a patch of hairs. Both endopods have three segments and are omitted here for clarity. The 2nd and 3rd exopodite segments are almost fused and only a faint line of separation remains. On the left side the 3rd exopodite segment has three small spines (the outer one is missing on the illustrated specimen); on the right the 3rd exopodite has one long curved spine and two of medium length.

REMARKS. Except for sexual differences these males agree so closely with the female *H. angusticeps* that there is no doubt that they are conspecific.

Haloptilus paralongicirrus Park, 1970

MATERIAL EXAMINED: 8 males and 160 females from 7 RMT 1 hauls made at 400–55 m depth in a position 18°N 25°W, between 12 and 16 November 1969. 5 males are deposited at the British Museum (Natural History), reg. no. 1974 : 649–653.

DESCRIPTION. Male (Fig. 24): Body length 1.67–2.20 mm with a mean of 1.87 mm (6 specimens). The shape of the cephalothorax is similar to that of the female. The head and 1st thoracic segment are fused, as are thoracic segments 4 and 5. In dorsal view the forehead is shaped like a rounded triangle, and in some specimens it is more rounded than shown here. The rostral filaments are fairly long and have swollen bases. The hind margin of the cephalothorax is smoothly rounded. The abdomen has five segments, the furcal rami are about twice as long as wide. The 1st antennae are longer than the body. The left 1st antenna is geniculate and has 21 segments; the proximal 12–13 segments have long sensory setae, segments 16, 17 and 18 have an undulating lamella, and segment 18 contains

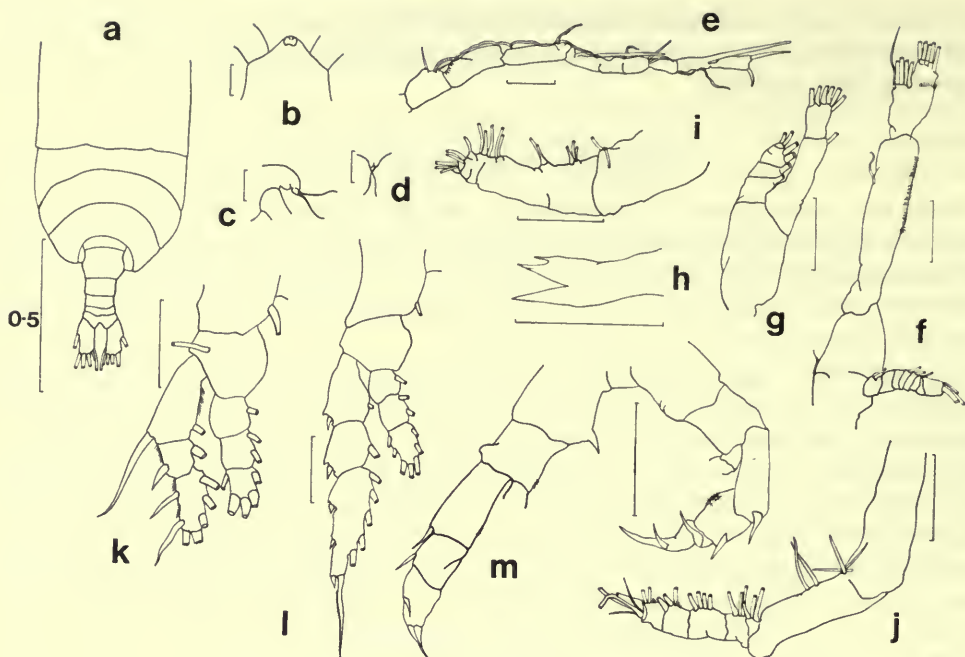


FIG. 24. *Haloptilus paralongicirrus* ♂. a, thorax and abdomen, dorsal; b, head, dorsal (different specimen); c, rostrum, lateral; d, rostrum, ventral; e, 1st antenna, segments 15-20; f, 2nd antenna; g, mandibular palp; h, mandible blade; i, 2nd maxilla; j, maxilliped; k, 1st leg; l, 2nd leg; m, 5th legs (different specimen). Bar scale 0.1 mm unless indicated.

the hinge joint. (The last segment is missing in the figure.) The remaining mouth-parts are very feebly chitinized and are similar in structure to those of the female. A satisfactory preparation of the 1st maxilla could not be made. The 2nd, 3rd and 4th pairs of legs are similar. The 5th pair of legs is slightly asymmetrical; the pointed projection on the 1st basipodite is larger on the left side, and the 2nd exopodite segment of the right leg bears a small haired lobe. Both endopodites have three segments and are omitted here for clarity.

REMARKS. *Haloptilus paralongicirrus* was described from the female (Park, 1970) and is closely related to *Haloptilus longicornis* (Claus, 1863) and *H. longicirrus* Brodsky, 1950. The females of the present species differ from those of *H. longicirrus* only in the shape of the forehead and their smaller size. Park suggested that these very slight differences may only be variations caused by differences in their vertical distributions - *H. longicirrus* living deeper than *H. paralongicirrus*. The present collections contain females of all three species and the males of two (that of *H. longicirrus* is unknown). *H. longicornis* was the shallowest of the three and *H. longicirrus* the deepest. The mean body lengths of *H. longicornis* were 2.14 mm (females) and 1.18 mm (males), of *H. paralongicirrus* they were 2.59 mm (females) and 1.87 mm (males), and of *H. longicirrus* 3.08 mm (females). All three species

were non-migrants. These results agree with those of Park (1970). The present males were found in association with female *H. paralongicirrus* and since their structure, body size and depth distribution accord with those of the female I believe that they are conspecific.

Euaugaptilus atlanticus sp. nov.

MATERIAL EXAMINED: 7 females and 2 males from 2 RMT 1 hauls made in a position 18°N 25°W; one, containing the female holotype, at 400–305 m depth on 17 November 1969 and the other, with the male allotype, at 400–300 m depth on 13 November 1969. Deposited at the British Museum (Natural History), holotype reg. no. 1974 : 654, paratypes reg. no. 1974 : 655–662.

DESCRIPTION. Female (Fig. 25a–g) : Body length 2.81–2.96 mm with a mean of 2.92 mm (7 specimens). The holotype measures 2.89 mm. The cephalothorax is long and slender and about 3.5 times as long as the 3-segmented abdomen. The head and 1st thoracic segment are separate but thoracic segments 4 and 5 are fused. In dorsal view the head protrudes slightly and is rounded. The rostrum has two fine short filaments. The hind margin of the cephalothorax is smoothly rounded. The genital segment is elongated and over twice as long as the combined length of the remaining two segments; it is slightly swollen laterally and more distinctly so ventrally. The furcal rami are about twice as long as wide; the inner furcal setae are almost as long as the cephalothorax.

The first antenna has 25 segments, the last five of which extend past the end of the body. The remaining mouthparts are as shown. The mandible blade has the same structure on both the right and left side. The swimming legs are identical in both sexes. The base of each external spine on the exopodite of the 1st leg has a conspicuous comb of curved spines. The terminal exopodite spine on the 2nd, 3rd and 4th leg is long and bears numerous small spinules. The 5th pair of legs is symmetrical. The 2nd basipodite has a very long seta which is longer than the remainder of the leg. The 2nd exopodite segment has a massive internal spine, carrying many coarse teeth, but no external spine. The endopodite has three segments.

Male (Fig. 25h–m) : The allotype is slightly crushed and could not be measured; the other male is 2.58 mm long. The general appearance is as for the female. The abdomen has five segments. The left 1st antenna is geniculate but broken in both specimens, the right 1st antenna reaches to the end of the furcal rami. The mouthparts are identical to those of the female except that the exopodite of the 2nd antenna has three terminal setae not two, and the mandible blade on the right side has a minute extra tooth. The swimming legs are as shown, the 4th leg is similar to the 3rd. The 5th pair of legs is slightly asymmetrical. The 1st exopodite segment of the left leg has no outer spine and the 3rd exopodite segment of this leg has a short claw and a long curved spine. On the right leg the second exopodite segment has a haired lobe on its inner edge, and the terminal segment has three spines. On both legs the inner corner of the 2nd basipodite bears a curious structure shaped like a segmented hemisphere. The endopodites of both legs have three segments.

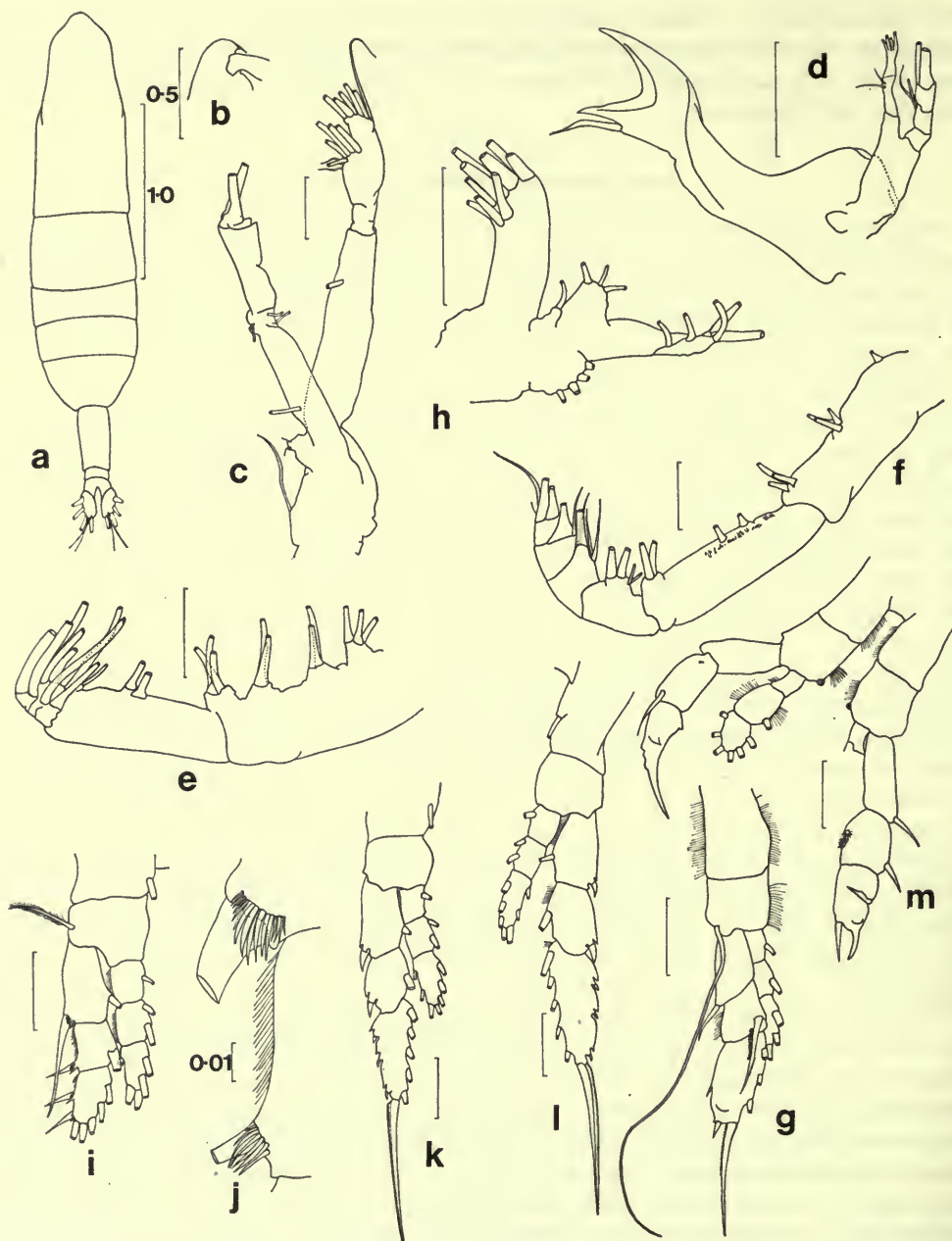


FIG. 25. a-g, *Euangaptilus atlanticus* ♀. a, body, dorsal; b, forehead and rostrum, lateral; c, 2nd antenna; d, mandible right side; e, 2nd maxilla; f, maxilliped; g, 5th leg. h-m, *Euangaptilus atlanticus* ♂. h, 1st maxilla; i, 1st leg; j, 1st leg, outer edge of exopodite segments 1 and 2; k, 2nd leg; l, 3rd leg; m, 5th legs. Bar scale 0.1 mm unless indicated.

REMARKS. The female of *E. atlanticus* resembles that of *E. longiseta* Grice & Hulsemann, 1965. I have examined the type specimen of this latter species at the British Museum (Natural History) and it differs from *E. atlanticus* in the structure of the mandible blade, the 1st leg and the 2nd exopodite segment of the 5th leg. The male of *E. longiseta* is smaller than the present species and has a different 5th pair of legs. The copepodite *E. sp. 1* Tanaka & Omori, 1974, is also similar to the present species but it is larger and differs in the structure of the 1st maxilla and mandible blade.

***Euaugaptilus fecundus* Tanaka & Omori, 1974**

Euaugaptilus sp. 3 Grice & Hulsemann, 1967 : 37, figs 231–240 ; Matthews, 1972 : 45.

MATERIAL EXAMINED : 1 female from an RMT 1 haul made at 1250–1000 m depth in a position 18°N 25°W on 17 November 1969. Deposited at the British Museum (Natural History), reg. no. 1974 : 663.

DESCRIPTION. Female (Fig. 26a–h) : Body length 6.40 mm. I was preparing to describe and name this specimen until I saw the recent account of *E. fecundus*. The present female differs from Tanaka & Omori's specimen only in the following minor details, (a) the endopod of the 2nd antenna is about 4 times longer than the exopod, instead of 2.6 times, (b) there are 24 setae on the endopod of the 2nd maxilla instead of 19, and (c) the 3rd endopodite segment of the 2nd leg has seven setae instead of six. The setation of the distal segments of the maxilliped is slightly obscure in the present female but in all other respects it is identical to *E. fecundus*.

REMARKS. I believe that this species is the female of the male described as *Euaugaptilus* sp. 3 by Grice & Hulsemann (1967). Except for the 1st antenna and 2nd maxilla the mouthparts of the present female are identical to those of the male. The 1st lobe of the 2nd maxilla bears a single seta in both the present female and that of Tanaka & Omori ; this is not shown by Grice & Hulsemann but it is easily damaged when the appendage is dissected off the body. The endopod of the 2nd maxilla in the present specimen has more setae than either the male or Tanaka & Omori's female. The proportions of the rami in the 2nd antenna are similar in the present female and the male. The endopodite of the 1st leg has three segments in the male but only two in both females ; the remaining swimming legs of the male are not described in detail by Grice & Hulsemann.

Except for normal sexual differences the only real difference between the females and the male is in the segmentation of the 1st leg. Intraspecific variation occurs in *Euaugaptilus*, however, both in the setation of the mouthparts and in the segmentation of the 1st leg (Matthews, 1972). Grice & Hulsemann (1967) and Matthews (1972) were unable to refer the male to a known species but pointed out similarities with *E. rigidus* (Sars, 1907). The true male of *E. rigidus* is described below (p. 357), and the agreement between the present female and the male *E. sp. 3* is so good that I have no doubt that they are conspecific.

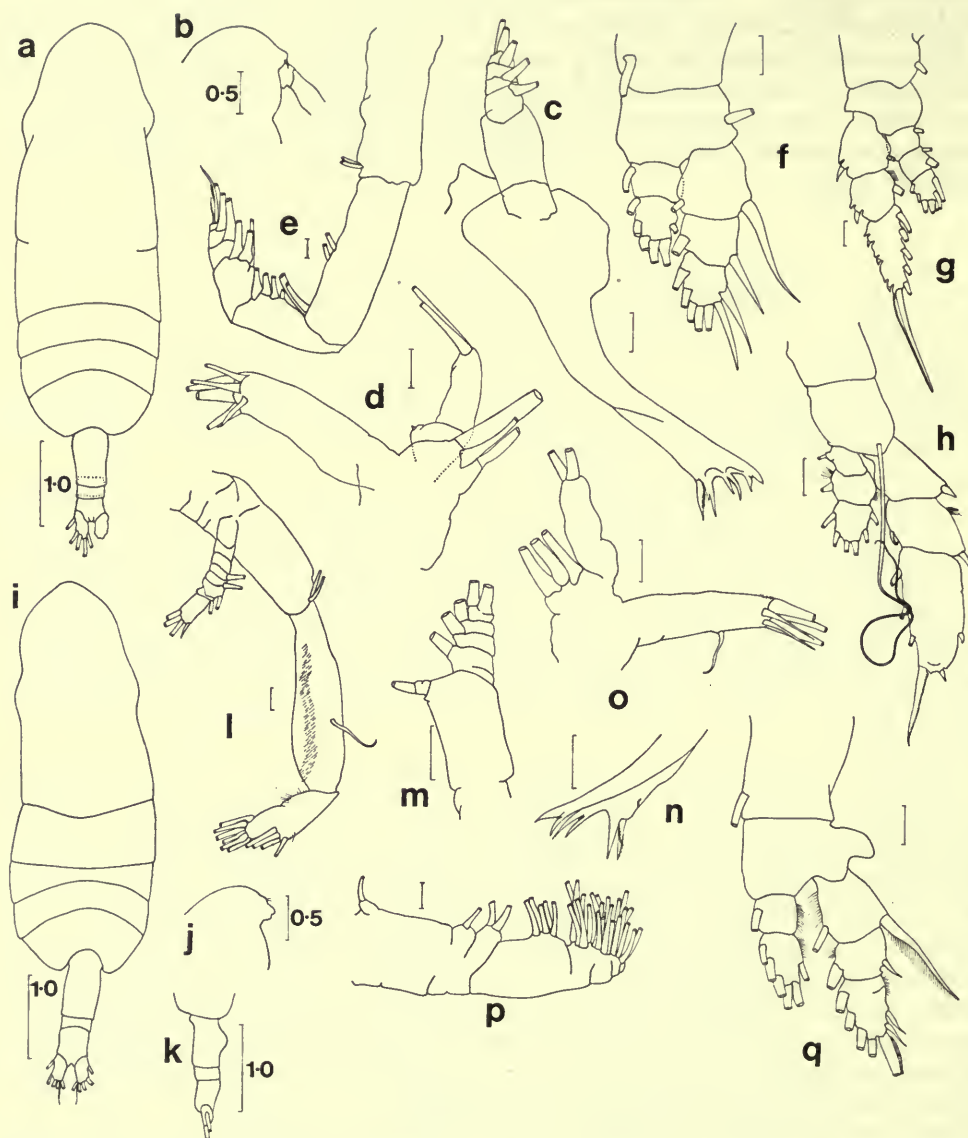


FIG. 26. a-h, *Euaugaptilus fecundus* ♀. a, body, dorsal; b, forehead and rostrum, lateral; c, mandible; d, 1st maxilla; e, maxilliped; f, 1st leg; g, 2nd leg; h, 5th leg. i-q, *Euaugaptilus latifrons* ♀. i, body, dorsal; j, forehead and rostrum, lateral; k, last thoracic segment and abdomen, lateral; l, 2nd antenna; m, mandibular palp; n, mandible blade; o, 1st maxilla; p, 2nd maxilla; q, 1st leg. Bar scale 0.1 mm unless indicated.

Euaugaptilus latifrons (Sars, 1907)

MATERIAL EXAMINED: 2 females from 2 N113H hauls made at 800–475 m depth off Fuerteventura (28°N 14°W) on 26 November 1965. 3 females from 2 RMT 1 hauls made at 700–505 m depth in a position 18°N 25°W, between 14 and 15 November 1969.

DISCUSSION. The present females (Fig. 26i–q) agree generally with the descriptions of Sars (1924, 1925), Sewell (1932) and, particularly, Tanaka & Omori (1974). There is tremendous variation in the number of setae on the 2nd maxilla in this species. Tanaka & Omori discussed this in relation to their specimen and those of Sars, Sewell and Vervoort (1965). The present females have the following numbers of setae on the various lobes of the 2nd maxilla:

Station no. of specimen	Lobes of 2nd maxilla						Endopod
	1	2	3	4	5	6	
7089 no. 16	1	0	1	2	5	6	16 (fig. 26p)
no. 16 (2nd specimen)	1	0	1	2	2	14	
no. 17 } same specimen	1	0	1	2	3	5	12 (right side)
no. 17 }	1	0	1	2	5	17	(left side)
5825 no. 4	1	0	1	2	3	17	
no. 1	1	0	1	2	2	4	8

In the 2nd maxilla of some of these females lobe 6 and the endopod cannot be distinguished, and in one specimen there is some variation between the left and right side. The present specimens measure 4.96–6.72 mm with a mean of 5.63 mm.

Euaugaptilus maxillaris Sars, 1920

MATERIAL EXAMINED: 3 females from 3 N113H hauls made at 960–550 m depth off Fuerteventura (28°N 14°W), between 24 and 28 November 1965. 3 females and 2 males from 3 RMT 1 hauls made at 785–610 m depth in a position 18°N 25°W, between 13 and 14 November 1969. 5 females and the males are deposited at the British Museum (Natural History), reg. no. 1974: 664–670.

DESCRIPTION. Female (Fig. 27a–g): Body length 3.27–5.76 mm with a mean of 5.11 mm (6 specimens). The cephalothorax is long and narrow and just over 3.5 times as long as the 3-segmented abdomen. The head and 1st thoracic segment are separate. The forehead and hind margin of the cephalothorax are rounded. The genital segment is 1.8 times as long as the combined length of the two subsequent segments. The 1st antenna has 25 segments and exceeds the body length by 4–5 segments. Except for the 1st maxilla the remaining mouthparts are as figured by Sars (1924). The distal setae of the 2nd maxilla and maxilliped have very small 'buttons'. The 1st maxilla (Fig. 27e, f) differs from the descriptions of Sars (1924, 1925) and Tanaka & Omori (1974) in the development of the endopodite. Both Sars' and Tanaka & Omori's specimens had a single endopodite segment with five setae. One of the females illustrated here has two endopodite segments bearing

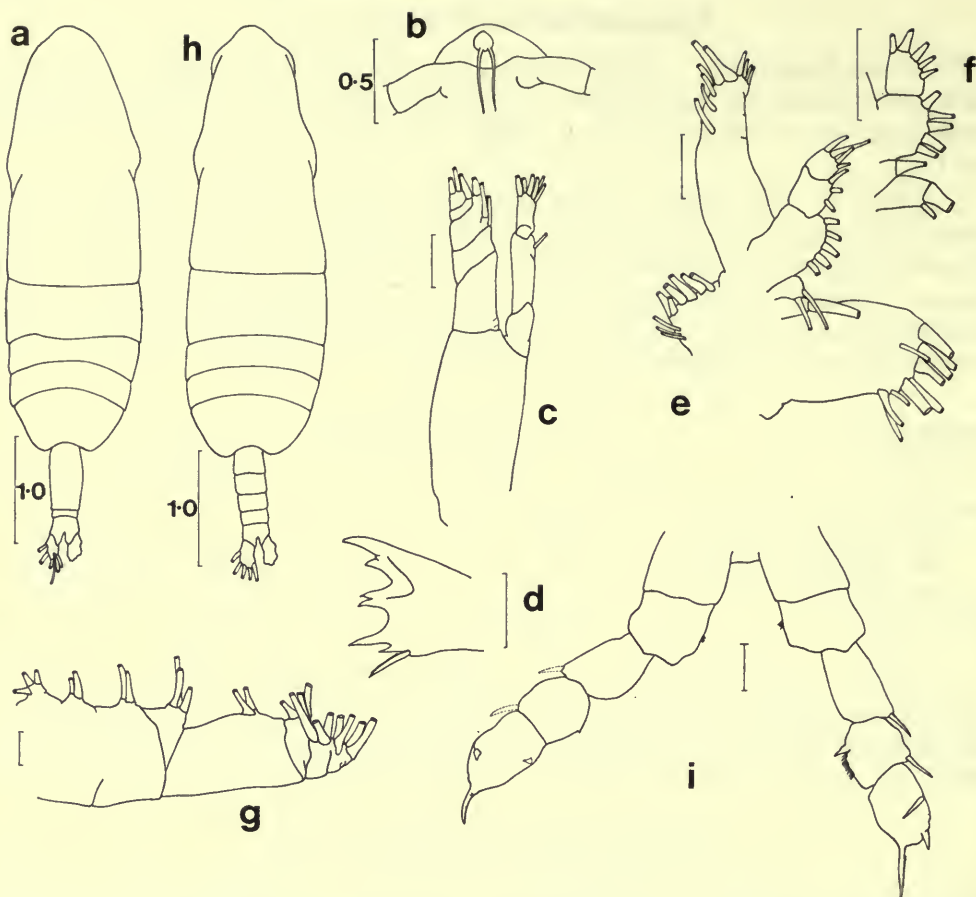


FIG. 27. a-g, *Euaugaptilus maxillaris* ♀. a, body, dorsal; b, rostrum, ventral; c, mandibular palp; d, mandible blade; e, 1st maxilla; f, 1st maxilla, small specimen; g, 2nd maxilla. h-i, *Euaugaptilus maxillaris* ♂. h, body, dorsal; i, 5th legs. Bar scale 0.1 mm unless indicated.

three and four setae (Fig. 27e). Both the segmentation and setation of this endopodite are subject to variation however, since two other specimens have only a single segment with six and seven setae respectively. The endopodite of the 1st maxilla of the smallest female (3.27 mm, Fig. 27f) agrees with Sars' account but the 2nd and 3rd endites have two and one setae respectively – the converse of the arrangement in both previous accounts and in the other specimens here. The swimming legs are as described by Sars.

Male (Fig. 27h, i): Body length 5.12 mm (both specimens). The cephalothorax is 3.5 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are separate; thoracic segments 4 and 5 are fused. In dorsal view the forehead protrudes more than in the female; the rostrum has two fairly long filaments. The furcal rami are twice as long as wide. The left 1st antenna is presumably

geniculate but is broken in both specimens; the right 1st antenna has 25 segments and exceeds the body length by five segments. The remaining mouthparts are identical to those of the present females. Both specimens have only a single endopodite segment in the 1st maxilla, carrying seven and eight setae respectively; otherwise this appendage is as shown in Fig. 27e.

The swimming legs are the same as in the female. The 5th pair of legs is slightly asymmetrical. The external exopodite spines on the left leg are missing in the illustrated specimen but present in the other. The 2nd basipodite segment of both legs has a small patch of spines. The endopodites are 3-segmented on both sides and are omitted here for clarity.

REMARKS. The female of *E. maxillaris* has only been described and figured by Sars (1924, 1925) and by Tanaka & Omori (1974). The male has hitherto been unknown. The present female specimens agree with these descriptions and I have no doubt that they are conspecific. The variation in structure of the 1st maxilla accords with the intraspecific variations noted in *Euaugaptilus* by Matthews (1972) and by Tanaka & Omori (1974). Similar differences are also present in several of the species described here.

Euaugaptilus ? *longicirrhus* (Sars, 1905)

MATERIAL EXAMINED: 1 female taken in an N113H fished at 800–680 m depth off Fuerteventura (28°N 14°W) on 26 November 1965. 3 females and 1 male from 2 RMT 1 hauls made at 500–410 m depth in a position 18°N 25°W, between 22 and 24 November 1969. 3 females and the male are deposited at the British Museum (Natural History), reg. no. 1974: 671–674.

DESCRIPTION. Female (Fig. 28a–c): Body length 4.18–4.56 mm with a mean of 4.31 mm (4 specimens). The general appearance of the body is as shown by Sars (1924). The rostral filaments are very long. Except for the 2nd maxilla the mouthparts of the present females are the same as those of the male, and fit Sewell's (1947) description better than Sars'. The mandibular palp is very reduced with the exopod having four and the endopod two setae; the blade has two more teeth than either Sars' or Sewell's specimens. The 1st maxilla is reduced and agrees with Sewell's description. The 2nd maxilla has 3 (2 long and 1 spike), 1, 2, 3, 2 and 3 setae on lobes 1–6 respectively, whereas Sars' specimen had –, 1, 2, 3, 3, 3 setae and Sewell's 2, –, 2, 3, 2 and 3. The legs all have 3-segmented exopods and endopods – the 1st pair thereby agreeing with Sewell's account rather than Sars'.

Male (Fig. 28d–h): Body length 3.42 mm. The cephalothorax is similar in shape to the female but has slightly more conspicuous shoulders. It is 3.7 times as long as the 5-segmented abdomen. Thoracic segments 4 and 5 are fused and the hind margin of the cephalothorax is rounded. The rostral filaments are very long. The left 1st antenna reaches to the end of the abdomen; it is geniculate and has 21 segments. The right 1st antenna is broken. The mouthparts are as shown and are identical to the female except that the 1st lobe of the 2nd maxilla has only one seta. The swimming legs are the same as in the female. The 5th pair of legs are slightly

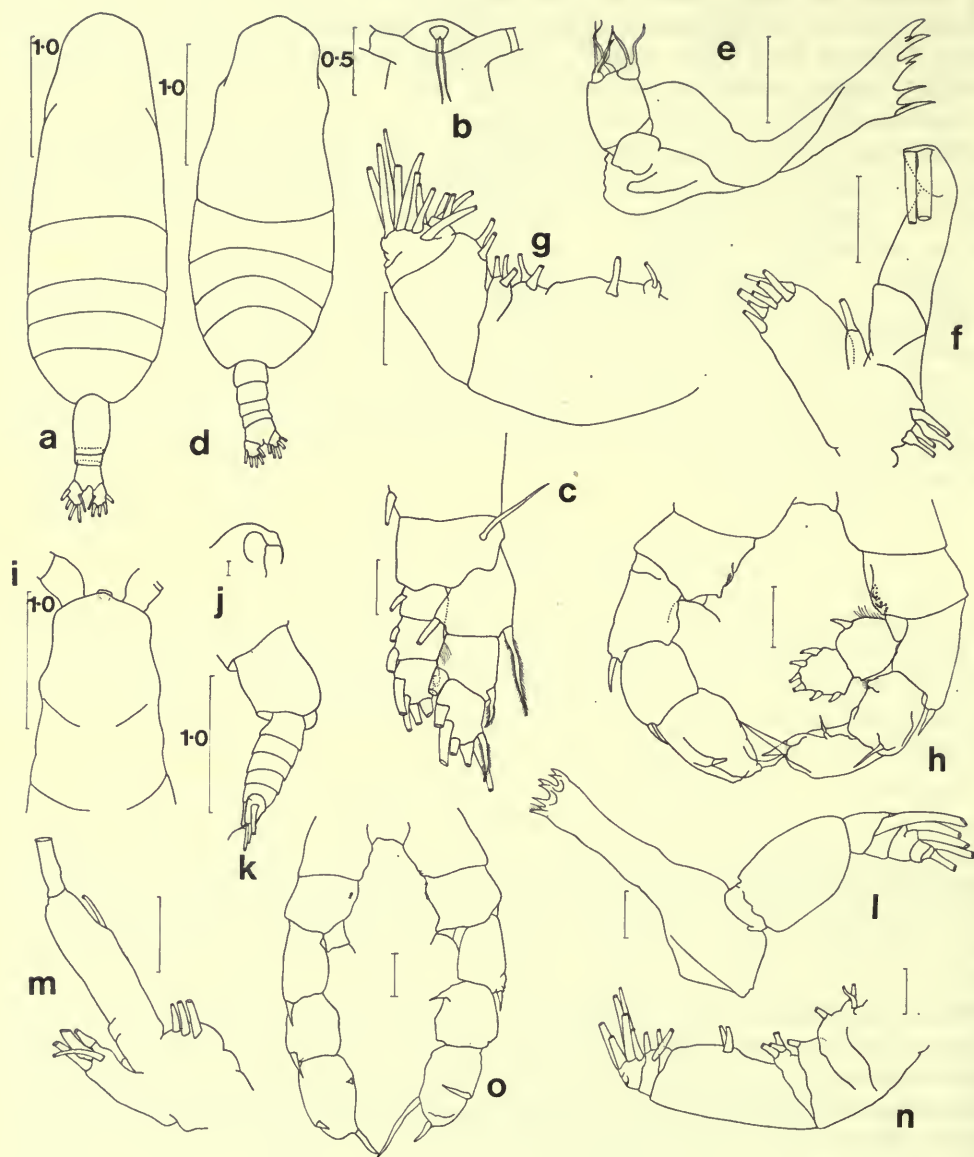


FIG. 28. a-c, *Euaugaptilus longicirrhus* ♀. a, body, dorsal; b, rostrum, ventral; c, 1st leg. d-h, *Euaugaptilus longicirrhus* ♂. d, body, dorsal; e, mandible; f, 1st maxilla; g, 2nd maxilla; h, 5th legs. i-o, *Euaugaptilus rigidus* ♂. i, head, dorsal; j, forehead and rostrum, lateral; k, last thoracic segment and abdomen, lateral; l, mandible; m, 1st maxilla; n, 2nd maxilla; o, 5th legs. Bar scale 0.1 mm unless indicated.

asymmetrical. The 2nd exopodite segment of the right leg has a small haired lobe ; the 2nd basipodite segment of both legs has a patch of raised spots on its internal edge. The endopods of both legs are 3-segmented.

REMARKS. *E. longicirrhus* was described by Sars (1924, 1925) from an adult female. The only other description is by Sewell (1947) who attributed a stage V female copepodite to this species. Matthews (1972) agreed with Sewell and kindly identified the present female taken off Fuerteventura (Roe, 1972*d*). The appendages of Sewell's specimen differ from those of Sars' in several respects – the exopodite of the 1st pair of legs has three segments not two, and the mandibular palp and 1st and 2nd maxillae differ in details of their setation. The present specimens show almost complete agreement with Sewell's account and if his copepodite is *E. longicirrhus* then the specimens described here are also this species.

Euaugaptilus rigidus (Sars, 1907)

MATERIAL EXAMINED : 2 females from 2 NI13H hauls made at 590–450 m depth off Fuerteventura (28°N 14°W), between 15 and 26 November 1965. 1 female and 1 male from 2 RMT 1 hauls made at 785–300 m depth in a position 18°N 25°W, between 13 and 14 November 1969. The male is deposited at the British Museum (Natural History), reg. no. 1974 : 675.

DESCRIPTION. Male (Fig. 28i–o) : Body length *c.* 4.3 mm but as the cephalothorax was fractured accurate measurements are impossible. The general appearance of the body, especially the shape of the head and hind margin of the cephalothorax, are as for the female. The head and 1st thoracic segment are separate but thoracic segments 4 and 5 are fused. The rostrum has two filaments of medium length. The abdomen has five segments ; the furcal rami are about 1.5 times as long as wide. The 1st antenna are broken off on both sides. Except for the 2nd maxilla the other mouthparts are identical to the female described by Sars (1924, 1925). On the present specimen the first six lobes of the 2nd maxilla bear 2, 1, 1, 3, 2 and 1 setae respectively ; whereas Sars' female had 1, 1, 1, 2, 2 and 1 setae on these lobes. Slight variation in the setation of this appendage occurs, however, since the female described by Tanaka (1964) had 2, 1, 1, 3, 2 and 2 setae and the present females have 2, 1, 1, 3, 2, 1 (two specimens) and 2, –, 1, 3, 2, 1 setae respectively. The first four pairs of legs are identical to the female. The 5th pair of legs is slightly asymmetrical. The 2nd exopodal segment of the right leg has a pointed lobe on its inner margin ; the outer spine of this segment is missing and apparently broken off. The 2nd basipodite segment of both legs has a small corrugated patch. The endopodite on both sides has three segments and is omitted for clarity.

REMARKS. The agreement between this specimen and the female is so good that I have no doubt that they are conspecific. The slight variation in setation of the 2nd maxilla is not surprising since Matthews (1972) found a considerable degree of intraspecific variation in this genus. Vervoort (1965) reported a damaged male of this species, measuring 4.30 mm, but it has hitherto been undescribed. The male *E. sp.* 3 of Grice & Hulsemann (1967) has been discussed earlier (p. 351).

Euaugaptilus mixtus (Sars, 1907)

Euaugaptilus propinquus Sars, 1920 : 17 ; 1924 : pl. 102 ; 1925 : 297 ; Rose, 1933 : 221, 230, fig. 283 ; Vives, 1970 : 554–555 ; 1972 : 221–222 ; Matthews, 1972 : 39 ; Tanaka & Omori, 1974 : 193, 197, 199, 200, 248–250, figs 3h, 26.

MATERIAL EXAMINED : 2 females in 2 N113H hauls made at 960–750 m depth off Fuerteventura (28°N 14°W), between 25 and 28 November 1965. 5 females taken in 5 RMT 1 hauls made at 900–410 m depth in a position 18°N 25°W, between 12 and 16 November 1969. 6 females are deposited at the British Museum (Natural History), reg. no. 1974 : 676–681.

DESCRIPTION. Female (Fig. 29h–o) : Body length 3.50–3.80 mm with a mean of 3.65 mm (7 specimens). The general appearance of the body is as shown by Sars (1924), Hulsemann (1967) and Tanaka & Omori (1974). The cephalothorax is 2.6 times as long as the 3-segmented abdomen. The head and 1st thoracic segment are separate ; thoracic segments 4 and 5 are fused. The forehead is rounded and the rostrum has two filaments of medium length. The hind margin of the cephalothorax is rounded in dorsal view but slightly angular when seen laterally. The genital segment is about 1.5 times as long as the combined length of the two subsequent segments. The furcal rami are twice as long as wide. The 1st antenna has 25 segments and exceeds the body length by 2–3 segments. The remaining mouthparts are as shown but there is slight variation in the setation of both the 2nd antenna and 1st maxilla, and in the number of mandibular teeth. The 2nd antenna was examined in three specimens, two of which had nine large setae on the endopodite and the 3rd (Fig. 29j) had eight. The 1st outer lobe of the 1st maxilla has six large and one small setae in three specimens, six large in one, five ? large in one, and five large and one small in another (Fig. 29m). The mandibular teeth are in groups of 2, 2 and 3 in four specimens (Fig. 29l), but in two of these four examples the second tooth of the middle group is minute and could easily be overlooked ; a further specimen has 2, 2 and 2 teeth, and another 2, 1 and 3. The distal setae of the 2nd maxilla and maxilliped have well-developed 'buttons'. The legs agree with previous descriptions.

REMARKS. *E. mixtus* was described briefly by Sars in 1907 from 'Princesse Alice' station 1794. It does not, however, appear in the list of copepods taken at this station in Sars (1925). The only other record of this species is by Lysholm & Nordgaard (1945). This specimen was probably identified by Sars and was re-described by Hulsemann (1967). *E. propinquus* was described briefly by Sars in 1920 and more fully in 1924 and 1925. It was recorded by Vives (1970, 1972) and a further description has recently been given by Tanaka & Omori (1974). Sars listed his specimens as coming from 'Princesse Alice' stations 1781, 2738 and 3021. I have borrowed a female specimen of *E. propinquus* from the Oceanographic Museum, Monaco, which was caught at station 1768 in 1904. This specimen is not mentioned by Sars and it is not on his list of species taken at this station.

Hulsemann (1967) pointed out the similarity between *E. mixtus* and *E. propinquus* and said that they could be distinguished by (a) a slightly different shaped forehead, (b) the mandibular tooth arrangement is 2, 1 and 3 in *E. mixtus* and 2, 2 and 2 in

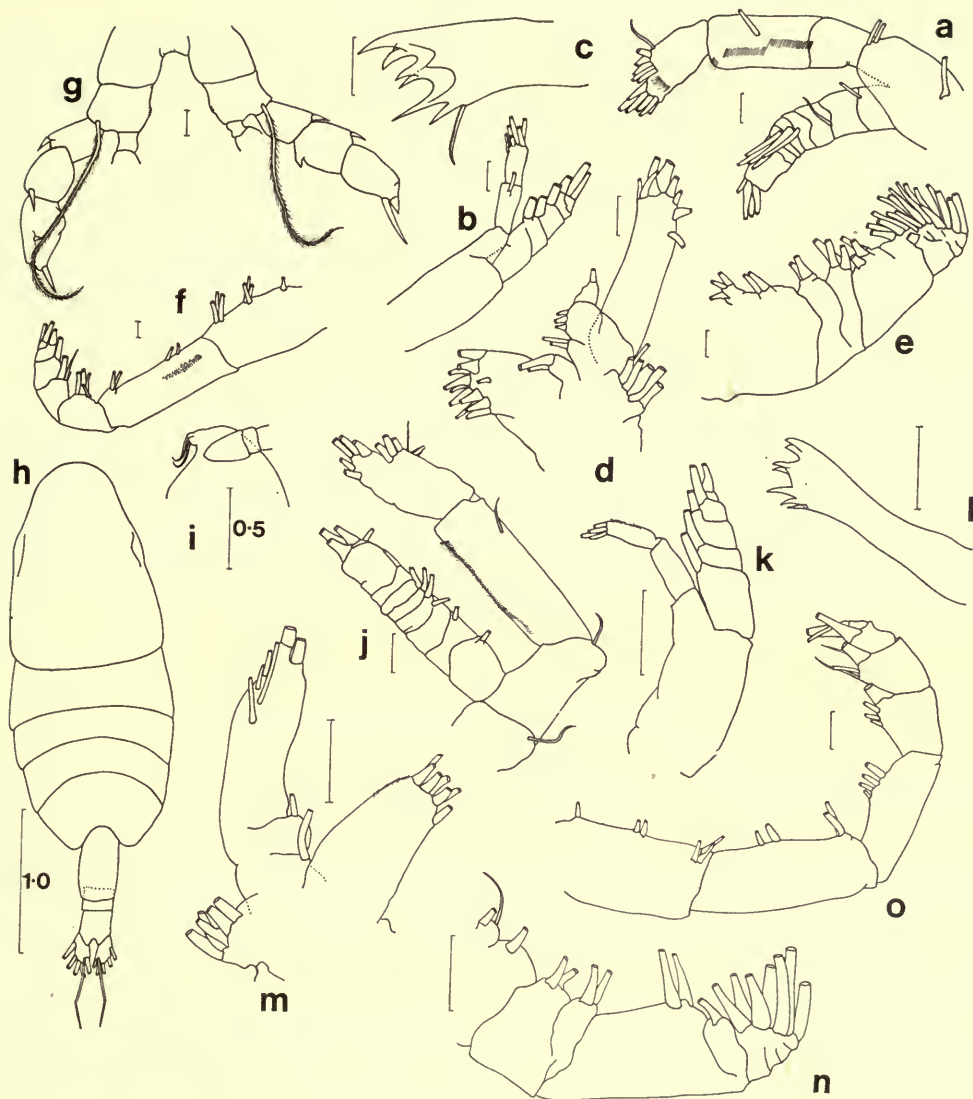


FIG. 29. a-g, *Euaugaptilus hyperboreus* ♂. a, 2nd antenna; b, mandibular palp; c, mandible blade; d, 1st maxilla; e, 2nd maxilla; f, maxilliped; g, 5th legs. h-o, *Euaugaptilus mixtus* ♀. h, body, dorsal; i, forehead and rostrum, lateral; j, 2nd antenna (different specimen); k, mandibular palp; l, mandible blade; m, 1st maxilla; n, 2nd maxilla; o, maxilliped (different specimen). Bar scale 0.1 mm unless indicated.

E. propinquus, and (c) the 1st maxilla of *E. mixtus* has one seta on the 2nd basipodite and six large setae on the exopodite, whereas these segments in *E. propinquus* have two setae and five large and one small seta respectively.

The female described by Tanaka & Omori (1974) is identical to the present 'Discovery' specimens. These latter females are intermediate between *E. mixtus* and *E. propinquus* (Roe, 1972d). In all of them the setation of the 1st maxilla agrees with that of *E. mixtus* but the arrangement of the mandibular teeth varies. One specimen has the pattern described by Hulsemann for *E. mixtus*, one that described by Sars for *E. propinquus*, and four have a varying and intermediate arrangement. Without dissection it is difficult to ascertain the setation of the 1st maxilla of the 'Princesse Alice' specimen. However, it definitely has five large and one small seta on the exopod but I could see only one seta on the 2nd basipodite. The mandibular tooth arrangement of this specimen differs from any described above and is 1, 1 and 4. The cephalothorax of this specimen is distorted and the shape of the forehead cannot be accurately determined.

The differences between these two species are very slight. The presence of an additional seta on the 1st maxilla and one of a different size seem well within the range of intraspecific variation seen in several *Euaugaptilus* spp. (for example, see p. 355). The shape of the forehead may well be variable and the mandibular tooth pattern certainly is. Furthermore, it is clear that the detailed structure of Sars' material was not uniform. I believe that there is no essential difference between *E. mixtus* and *E. propinquus* and that they are synonymous.

Euaugaptilus hyperboreus Brodsky, 1950

Euaugaptilus hyperboreus ? ; Roe, 1972a : 299, 311 ; 1972d : 1035.

E. elongatus ; Roe, 1972a : 299, 306, 311.

MATERIAL EXAMINED : 2 females and 1 male taken in 3 NI13H hauls made at 950–600 m depth off Fuerteventura (28°N 14°W), between 26 and 28 November 1965. 2 females taken in 2RMT 1 hauls made at 1220–800 m depth and 1 female in an RMT 8 fished at 1020–910 m in a position 18°N 25°W, between 14 and 18 November 1969.

DISCUSSION. Tanaka & Omori (1974) have recently clarified the differences between this species and *Euaugaptilus elongatus* (Sars, 1905). In the course of the present work I borrowed a male and a female specimen of *E. elongatus* from the Oceanographic Museum, Monaco, both of which were taken at 'Princesse Alice' station 1781 on 21 August 1904. These specimens and the present 'Discovery' material confirm the differences in the setation of the 1st and 2nd maxillae observed by Tanaka & Omori. These differences are shown in Table 1.

Slight variation occurs in the setation of the 1st maxilla endopodite of *E. hyperboreus*, but none of the present specimens, nor those examined by Tanaka & Omori, have three setae on this lobe. Some differences are also present in the setation of the 2nd basipodite of the 1st maxilla, where the 'Discovery' male (Fig. 29a–g) has

TABLE I

The number of endopodite setae on the 1st and 2nd maxillae of
Euaugaptilus hyperboreus and *E. elongatus*

Specimen	Species	1st maxilla	2nd maxilla
'Princesse Alice' Station 1781 ♀	<i>E. elongatus</i>	3	8
'Princesse Alice' Station 1781 ♂	<i>E. elongatus</i>	3	8 (right) 9 (left)
'Discovery' station 5825 no. 7 ♀	<i>E. hyperboreus</i>	2	15
'Discovery' station 5827 no. 3 ♀	<i>E. hyperboreus</i>	2	15
'Discovery' station 5827 no. 4 ♂	<i>E. hyperboreus</i>	1	15
'Discovery' station 7089 no. 12 ♀	<i>E. hyperboreus</i>	1	15
'Discovery' station 7089 no. 14 ♀	<i>E. hyperboreus</i>	1	14
'Discovery' station 7089 no. 34 ♀	<i>E. hyperboreus</i>	2	14

three setae on the left side (Fig. 29d) but four on the right. Similar variation occurs on the endopod of the 2nd maxilla of the male *E. elongatus* from Monaco (Table 1). The specimens of *E. hyperboreus* have a spinous ridge at the base of the external exopodite spines of the 1st leg as described by Tanaka & Omori. Although closely related, these two species show consistent differences, especially in the number of endopodite setae on the 2nd maxilla. They should, I believe, be maintained as separate species.

Family BATHYPONTIIDAE

Bathypontia sarsi Grice & Hulsemann, 1965

Bathypontia minor Sars, 1907: 27; 1924: pl. 127; 1925: 360; Lysholm & Nordgaard, 1945: 42; Wilson, 1950: 171, fig. 303; Owre & Foyo, 1964a: 343; 1964b: 367; 1967: 100, figs 720–722, 724–726; 1972: 494; Tanaka, 1965: 379.

MATERIAL EXAMINED: 2 females and 3 males from 5 RMT 1 hauls made at 1250–700 m depth in a position 18°N 25°W, between 14 and 18 November 1969. Deposited at the British Museum (Natural History), reg. no. 1974: 682–686.

DESCRIPTION. Female (Fig. 30a–i): One specimen is 3.04 mm in length and the other is too badly damaged to measure. The cephalothorax is oval and 2.9 times as long as the 4-segmented abdomen. The head and 1st thoracic segment are separate, as are thoracic segments 4 and 5. The rostrum is large, rounded and curved downwards; it has no filaments or points. The last thoracic segment is symmetrical with ventrally directed points. The 2nd and 3rd abdominal segments have small spines on their hind margins. The furcal rami are slightly longer than wide. The 1st antenna has 23 segments and reaches to the hind edge of the genital segment. The remaining mouthparts are as shown. The mandible blade has a large tooth (Fig. 30d). The left 2nd maxilla has only five large hooked setae (Fig. 30f), but the right one has seven. Swimming legs 1–4 are similar to those of the male. The external exopodite spines on the 2nd pair of legs are symmetrical. The 5th pair of legs is uniramous with three segments on each side; the terminal segment

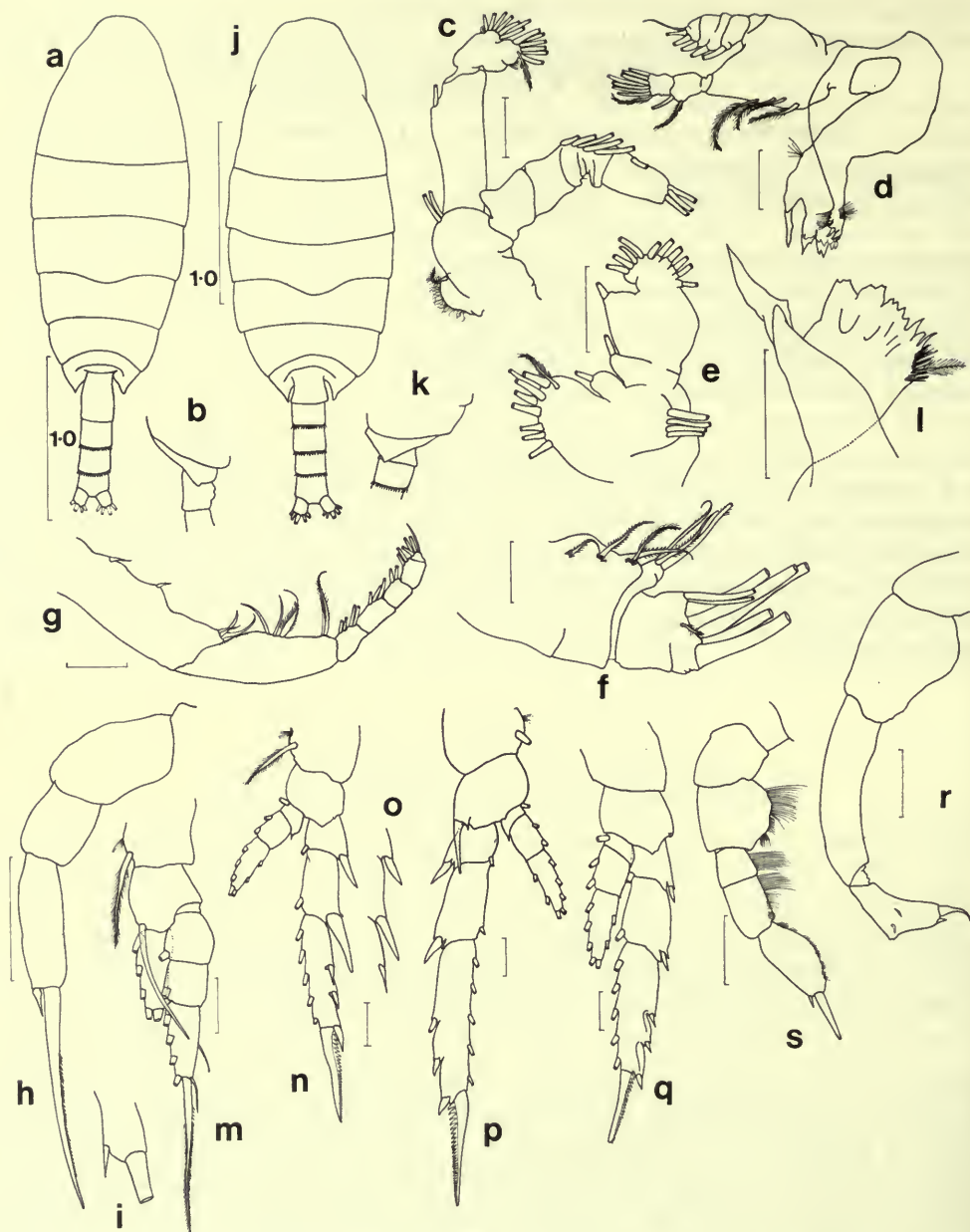


FIG. 30. a-i, *Bathypontia sarsi* ♀. a, body, dorsal; b, last thoracic segment, lateral; c, 2nd antenna; d, mandible; e, 1st maxilla; f, 2nd maxilla, left; g, maxilliped; h, 5th leg; i, 5th leg, other specimen. j-s, *Bathypontia sarsi* ♂. j, body, dorsal; k, last thoracic segment, lateral; l, mandible blade; m, 1st leg; n, 2nd leg, left; o, 2nd leg, outer edge of right exopodite; p, 3rd leg; q, 4th leg; r, 5th leg, right; s, 5th leg, left. Bar scale 0.1 mm unless indicated.

has one long and one short spine. The arrangement of these spines is slightly asymmetric in one specimen (Fig. 30i), but in the other both sides are as shown in Fig. 30h.

Male (Fig. 30j-s): Body length 2.74–3.04 mm with a mean of 2.91 mm (3 specimens). The general appearance of the body is the same as the female. The abdomen has five segments. The 1st antenna reaches to the end of the cephalothorax. The right 1st antenna is geniculate and has 20 segments. The remaining mouthparts are identical to those of the female but the right 2nd maxilla has seven large setae and the left only six. The swimming legs are as shown. The external spine on the 2nd exopodite of the 2nd pair of legs is slightly larger on the left side. The 5th pair of legs is uniramous and completely asymmetrical. The right leg (Fig. 30r) is longer than the left and has four segments; the last segment is roughly triangular in shape, terminates in two unequal spines, has a central pore and has a small lamella in the distal corner. The left leg (Fig. 30s), has five segments of which segments 2–5 have bundles of hairs of varying length; the 5th segment terminates in one long and one short spine.

REMARKS. *B. sarsi* is a very rare species which has never previously been fully described or figured. Sars (1924, 1925) gave the most complete account, and to verify the identification of the present specimens I borrowed a female and a male *B. sarsi* from the collections of the Oceanographic Museum, Monaco. The female was taken at 'Princesse Alice' station 1871 in 1904, but this specimen is not mentioned by Sars, nor is station 1871 included in his station list. The male has no station number or date but it was probably taken on a cruise to the Azores in 1904–5 (G. Testa, pers. comm.). These omissions add to the existing confusion surrounding Sars' station listings for this species (Owre & Foyo, 1964b).

The present 'Discovery' specimens differ from Sars' description in the shape of the last thoracic segment and possibly in the structure of the mandible blade. The 5th thoracic segment of these specimens has a fairly blunt ventrally directed point, whereas Sars figures this as being very sharp and directed straight back. In the 'Princess Alice' male, however, this point is identical to that of the 'Discovery' specimens (Fig. 30k), and in the 'Princess Alice' female it is also blunt but does go straight backwards. Sars described the mandible blade as having an external tooth which is only a little larger than the two following teeth. This tooth on the present 'Discovery' specimens seems to be larger than described by Sars but it is difficult to be certain. Owre & Foyo's (1967) photograph of the mandible blade shows no external tooth. It is impossible to see the mandible blade on either of the 'Princess Alice' specimens without dissection. The remaining mouthparts and the swimming legs of *B. sarsi* have never been described. In these 'Discovery' specimens they are very similar to those of *B. similis* Tanaka, 1965. The female 5th pair of legs agrees with previous accounts. Their asymmetry in one specimen approaches the condition seen in *B. intermedia* Deevey, 1973. *B. sarsi* and *B. intermedia* differ in several other respects, however, and presumably the slight asymmetry seen here is merely a variation similar to that shown in the setation of the 2nd maxilla. The 'Discovery' male's 5th pairs of legs are identical to that of the 'Princess Alice' male. All differ from Sars' figure in the shape of the last segment of

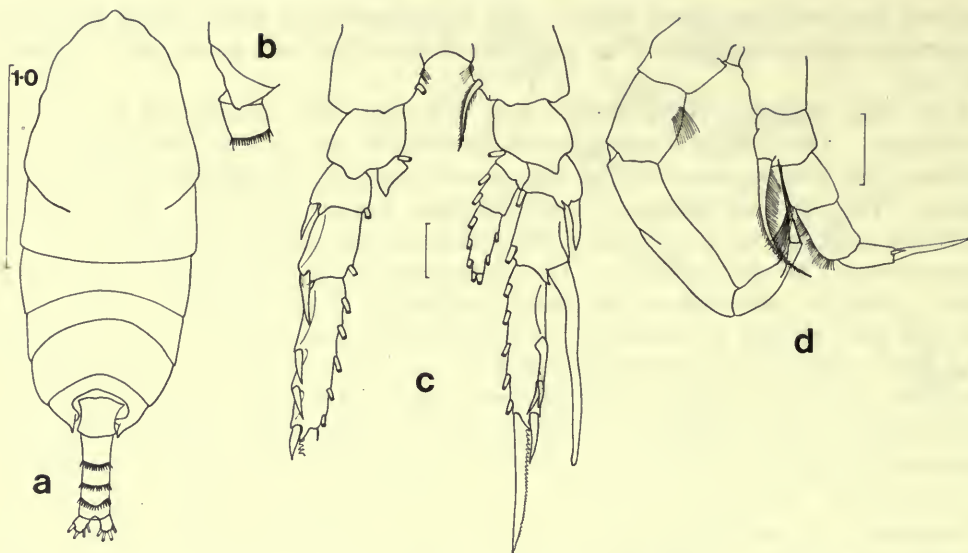


FIG. 31. *Bathypontia spinifera* ♂. a, body, dorsal; b, last thoracic segment, lateral; c, 2nd legs; d, 5th legs. Bar scale 0.1 mm unless indicated.

the right leg, but this is probably due to a difference in the angle at which Sars' figure was drawn.

***Bathypontia spinifera* A. Scott, 1909**

Bathypontia sarsi; Wheeler, 1970: 12, figs 77–90.

MATERIAL EXAMINED: 1 male taken in an RMT 1 fished at 700–610 m depth in a position 18°N 25°W on 14 November 1969.

DESCRIPTION. Fig. 31 shows the very characteristic 2nd pair of legs and the 5th pair of legs of the male *B. spinifera*.

REMARKS. Deevey (1973) pointed out the overall similarity between *B. spinifera* and *B. similis* Tanaka, 1965. Dr Tanaka kindly sent me some specimens of *B. similis*, the male of which can easily be distinguished from *B. spinifera* as it does not have the very long spine on the right 2nd leg. The present specimen measured 2.66 mm.

Incertae sedis

'*Xanthocalanus*' paululus Park, 1970

? *Amallothrix robustipes* Grice & Hulsemann, 1965: 239, fig. 13f–k; 1967: 26; Bradford, 1973: 147.

MATERIAL EXAMINED: 23 females and 2 males taken in 4 RMT 1 hauls made at 1250–800 m depth in a position 18°N 25°W, between 12 and 18 November 1969.

9 females and the males are deposited in the British Museum (Natural History), reg. no. 1974 : 687-697.

DESCRIPTION. Female (Fig. 32a-n) : Body length 1.14-1.29 mm with a mean of 1.22 mm (19 specimens). The cephalothorax is oval and 4.8 times as long as the 4-segmented abdomen. The head and 1st thoracic segment are almost completely fused but the 4th and 5th thoracic segments are separate. The head is characteristically helmet-shaped ; there are no apparent rostral filaments. The 5th thoracic segment protrudes laterally and is indented. The genital segment is longer than the combined length of the three subsequent segments. The furcal rami are about twice as long as wide. The 1st antenna reaches to the hind edge of the genital segment. In the 2nd maxilla, lobes 4 and 5 each have a large curved seta armed with teeth, and the endopodite has six setae of which at least two are plumose but none, as far as can be seen, are brush-like. The remaining mouthparts and the legs are as shown.

Male (Fig. 32 o-r) : Body length 1.29-1.37 mm. The cephalothorax is 3.2 times as long as the 5-segmented abdomen. The head and 1st thoracic segment are separate, as are thoracic segments 4 and 5. In lateral view the head is the same shape as in the female ; there are no rostral filaments. The 1st antenna has 22 segments and exceeds the body length by 2-3 segments. Some of the mouthparts are reduced as follows. The mandible blade is smaller than that of the female. The 1st maxilla has fewer setae on almost all lobes - 5 on the 1st outer lobe, 2 on the exopod, and 1, 1 and 3 on the 3rd, 2nd and 1st inner lobes respectively. All the setae except those on the outer lobe are very small and feeble. The 2nd maxilla has small, weak setae on all five lobes with a single larger seta on the 5th lobe ; the endopod has six sensory seta, all of which are, apparently, worm-like. The 1st basipodite of the maxilliped has fewer setae than in the female. Legs 1-3 are identical to those of the female ; the 4th pair of legs is broken in both specimens. The 5th pair of legs is asymmetrical and reaches back to the middle of the abdomen. The right leg has a 2-segmented exopodite and one short endopodite segment. In the left leg the endopodite is also only a single segment but it is almost as long as the 3-segmented exopodite ; the 2nd exopodal segment has a lamella which partially overlaps the 3rd segment ; this last segment bears clusters of hairs of varying length.

REMARKS. Despite the reduction in their mouthparts the present males are so similar to the females in the curious shape of the head and the structure of the swimming legs that I believe that they are conspecific. The present females differ from Park's (1970) description in only a few details. Park's specimens had one more seta on the 1st maxilla, two more on the endopod of the 2nd maxilla, longer 1st antennae and two fine rostral filaments. I could see no rostral filaments on the present specimens but this, together with the differences in setation, may be due to the difficulties in accurately observing these. Overall agreement is so good, however, that there is little doubt that they are the same species.

X. paululus is very similar to *Amallothrix robustipes* Grice & Hulsemann, 1965. I have examined the type of this latter species in the British Museum (Natural History). The shape of the cephalothorax is the same as that of the present females but unfortunately the slide(s ?) of the appendages is not in the Museum's collection.

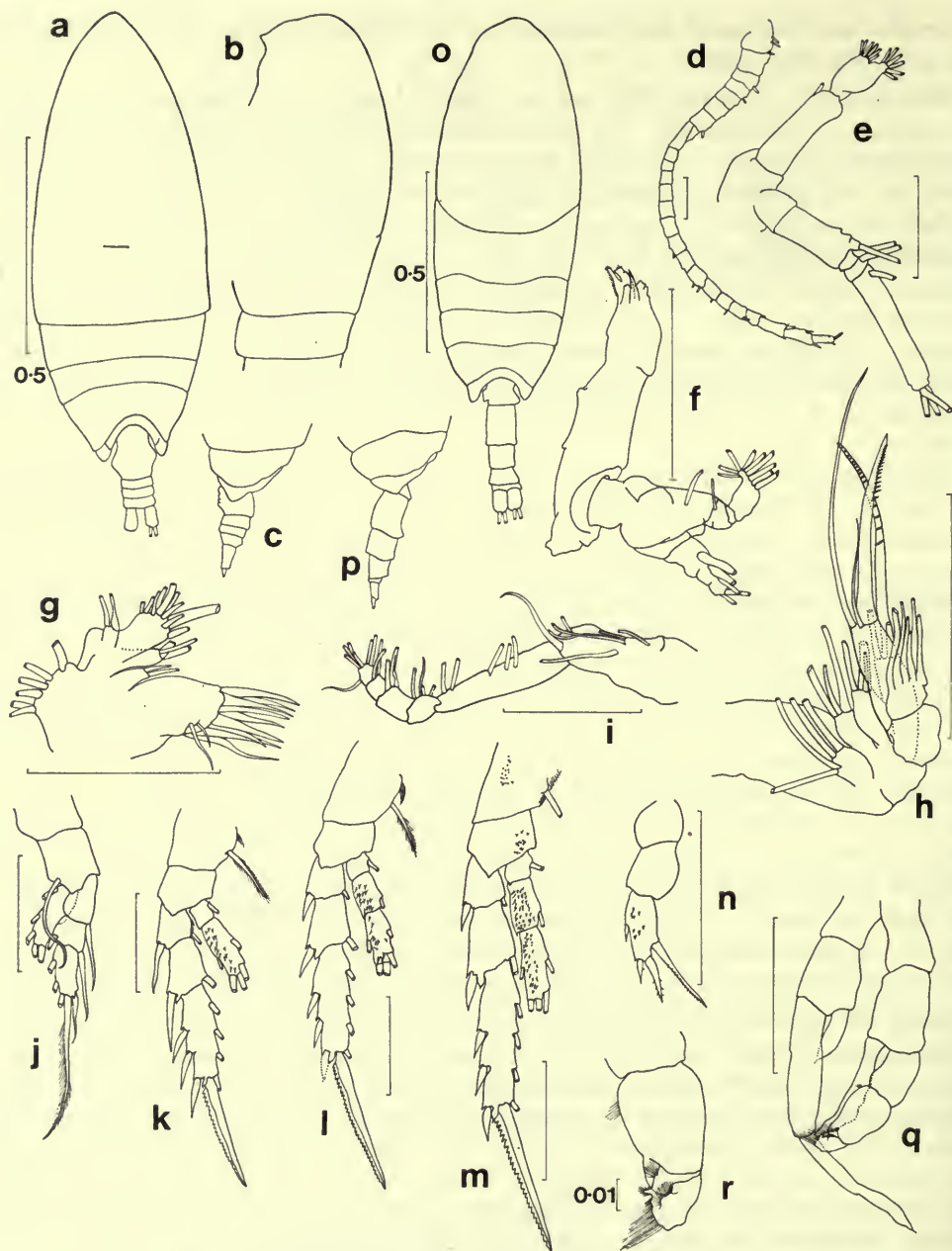


FIG. 32. a-n, '*Xanthocalanus*' *paululus* ♀. a, body, dorsal; b, head, lateral; c, last thoracic segment and abdomen, lateral; d, 1st antenna; e, 2nd antenna; f, mandible; g, 1st maxilla; h, 2nd maxilla; i, maxilliped; j, 1st leg; k, 2nd leg; l, 3rd leg; m, 4th leg; n, 5th leg. o-r, '*Xanthocalanus*' *paululus* ♂. o, body, dorsal; p, last thoracic segment and abdomen, lateral; q, 5th leg; r, 5th leg, exopodite segments 2+3 left leg. Bar scale 0.1 mm unless indicated.

Of the mouthparts of *A. robustipes* only the 1st antenna and the 1st maxilla have ever been described (Grice & Hulsemann, 1965, 1967). The 1st maxilla is very similar to that of the present species, and the swimming legs are apparently identical except for the absence of small spines on the endopod of the 2nd leg. The 5th leg differs in having the terminal spine longer than the internal spine. Without a description of the remaining mouthparts, however, especially the 2nd maxilla, it is impossible to ascertain whether or not *A. robustipes* and *X. paululus* are synonymous.

At the moment it is not possible to place this species into any of the four families which have sensory setae on the endopod of the 2nd maxilla. Bradford (1973) was unable to assign either *A. robustipes* or *X. paululus* to either the Phaennidae or the Scolecithricidae. This discovery of the male *X. paululus* confirms her opinion. This species differs from both these families (as defined by Bradford) in the following respects: (a) the endopod of the 2nd maxilla apparently lacks any brush-like setae, (b) there are no large spines on the posterior surfaces of the swimming legs, and (c) the male 5th pair of legs are biramous and have symmetrical basipodites. The presence of enlarged setae on lobes 4 and 5 of the 2nd maxilla further distinguishes it from the Scolecithricidae. It is distinct from the Diaixidae and Tharybidae in having reduced mouthparts in the male. It is further distinguished from the Diaixidae by the female possessing a 5th pair of legs and by the relatively simple nature of the male 5th legs.

This species is apparently closest to the Tharybidae but pending a revision of this family in relation to the three others mentioned here it seems advisable to record it as *incertae sedis*. To avoid any future additional synonymy I have retained the generic name *Xanthocalanus* for this species although it is certainly not of this genus, nor, if *A. robustipes* is synonymous, of *Amallothrix* either.

Species 1

MATERIAL EXAMINED: 2 females taken in 2 RMT 1 hauls made in a position 18°N 25°W; one at 1010–900 m depth on 13 November 1969 and the other at 900–800 m on 14 November 1969. Deposited at the British Museum (Natural History), reg. no. 1974: 698–699.

DESCRIPTION. Female (Fig. 33): Body length 1.29 mm and 1.44 mm. The cephalothorax is oval and about 5 times longer than the 4-segmented abdomen. The head and 1st thoracic segment are separate, as are thoracic segments 4 and 5. The rostrum is a curved spike containing a central groove – presumably it is formed of two more or less fused filaments. The last thoracic segment is slightly produced laterally. The 1st antennae are broken in both specimens. The other mouthparts are as shown. The illustrated 1st maxilla (Fig. 33f) has a damaged 1st outer lobe; the other 1st maxilla of the same specimen has seven large and two small setae on this lobe. In the 2nd maxilla all the lobes are at the distal end of the appendage. Lobe 4 has three large curved setae, furnished with many small spines, lobe 5 has two such setae and two small ones. The endopodite has eight long thin filaments which, as far as can be seen, all taper to a fine point; none of them is brush-like. The 1st leg has a long curved spine on the outer edge of each exopodite segment.

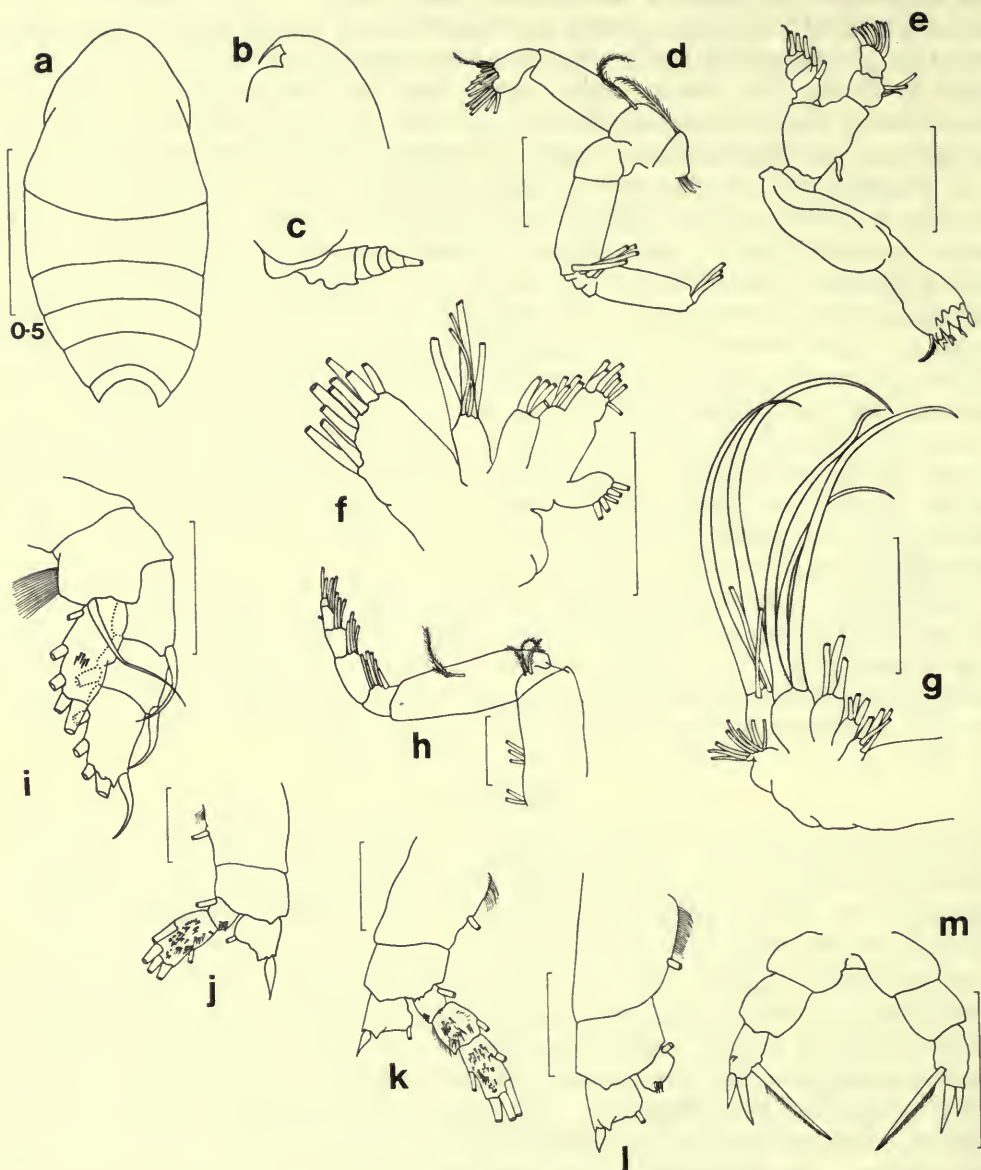


FIG. 33. Species 1 ♀. a, body, dorsal; b, forehead and rostrum, lateral; c, last thoracic segment and abdomen, lateral; d, 2nd antenna; e, mandible; f, 1st maxilla; g, 2nd maxilla; h, maxilliped; i, 1st leg; j, 2nd leg; k, 3rd leg; l, 4th leg; m, 5th legs. Bar scale 0.1 mm unless indicated.

Legs 2 to 4 are incomplete but the endopodites of legs 2 and 3 are covered with fairly large spines. The 5th pair of legs is small and uniramous. Each side has three segments, the third having a long internal spine and two shorter stout spines; on one side the surface of the 3rd segment has two small spines.

REMARKS. As with the preceding species I am unable to identify these females with any of the four families having sensory setae on the 2nd maxilla endopod. These setae are all simple and worm-like in the present specimens, thereby excluding them from either the Phaennidae or Scolecithricidae according to Bradford (1973). The presence of a 5th pair of legs distinguishes them from the Diaixidae. They may be members of the Tharybidae but as their legs are incomplete it is impossible to be certain. It seems best to record them as *incertae sedis* until complete specimens are found.

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A REVISION OF THE SPECIES OF
LAFOEIDAE AND HALECIIDAE
(COELENTERATA: HYDROIDA)
RECORDED FROM BRITAIN
AND NEARBY SEAS

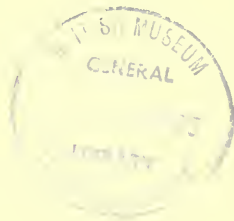
P. F. S. CORNELIUS

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BY
PAUL FREDERICK SINEL CORNELIUS

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A REVISION OF THE SPECIES OF LAFOEIDAE AND HALECIIDAE (COELENTERATA: HYDROIDA) RECORDED FROM BRITAIN AND NEARBY SEAS

By P. F. S. CORNELIUS

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SYNOPSIS

Nominal species of hydroids belonging to the families Lafoeidae and Haleciidae recorded from Britain and neighbouring seas are revised. Three species of Lafoeidae and nine species of Haleciidae are accepted.

INTRODUCTION

IDENTIFICATION guides covering the Hydroida faunas of the majority of countries bordering the southern North Sea have appeared during the last fifty years (Broch, 1927, 1928 ; Kramp, 1935 ; Vervoort, 1946 ; Leloup, 1952). In contrast the most

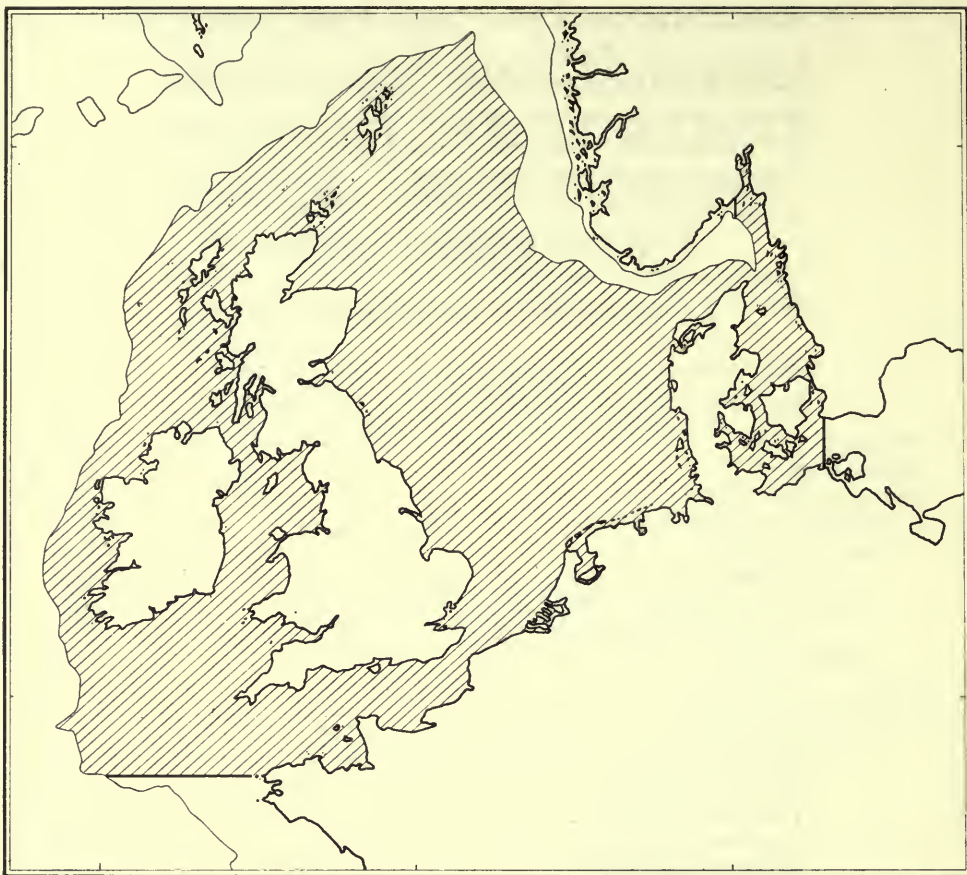


FIG. 1. Map of part of western Europe showing the faunal area (cross-hatching), delimited in most places by the 100 fm (183 m) depth contour (continuous thin line).

recent work describing all the hydroids of British coastal waters is that of Pennington (1885) in which the hydroid chapters were based largely on the monographs of Hincks (1868) and Allman (1871). Perhaps owing to the excellence of its illustrations Hincks' somewhat outdated work still often serves as an identification guide to the British thecate hydroids. The large amount of European work produced during the present century makes a systematic revision of the British hydroids now timely, and two of the thecate/leptomedusan families are revised here.

All nominal taxa of hydroids of the families Lafoeidae and Haleciidae recorded from the area defined below are evaluated. No new species are proposed. Indeed, it seems necessary to interpret the specific limits of some species more widely than hitherto, and some features previously regarded as good specific characters are shown to be unreliable.

A redefinition of the family Lafoeidae was given recently by Naumov (1960, 1969). He did not, however, treat the genus *Hebella* Allman (1888 : 39), which has unclear affinities. It has variously been included in the families Campanulariidae (by Allman, 1888) and Lafoeidae (by Ralph, 1958 ; Vervoort, 1968, 1972), and removed to a separate family, the Hebellidae (by Nutting, in Fraser, 1912 ; Nutting, 1927 ; Fraser, 1937, 1944, 1946). The Hebellidae was established to accommodate genera with separate gonothecae, a hydrothecal diaphragm and a conical hypostome to the hydranth (said to be spherical in Campanulariidae). The two originally included genera, *Hebella* and *Scandia* Fraser (1912 : 371), were separated as having respectively free medusae and fixed sporosacs. It seems logical at present to retain the family Hebellidae to accommodate these two genera, which are implicitly excluded from the Lafoeidae in Naumov's diagnosis also. The British records of *Hebella* are discussed below under *Lafoea dumosa*. None appears valid.

The faunal area outlined in Fig. 1 corresponds approximately with the continental shelf. Unavoidably it is arbitrary, some species being limital and none restricted to it. It was found that to include the whole of the English Channel, southern North Sea and all Danish waters would add only a few species to the list of all thecate hydroids known from Britain, whereas to include the coast of Norway would add sub-arctic species. Oslofjord and the whole of the Swedish west coast are included. To the south the latitude of the Isle d'Ouessant (Ushant) forms the boundary, so that the whole of the English Channel is included ; while to the west, north and north-east the 183 m (600 ft) depth contour provides the arbitrary limit. Taking the thecate hydroid fauna as a whole there appears to be only a few species confined to the deeper parts of the area thus defined, and the British species form, therefore, a recognizable continental shelf assemblage.

The material used was drawn mainly from the collections of the British Museum (Natural History), and carries registered numbers of the format 1894.3.5.11. The numbers reflect the approximate dates, in reverse, on which the specimens were registered and not the dates of collection or deposition in the Museum. Specimens loaned from other museums are so indicated.

Scientific names of British algae mentioned follow the checklist of Parke & Dixon (1968).

Family LAFOEIDAE Hincks, 1868

DIAGNOSIS. Colony stolonal or erect and branching ; hydrothecae tubular, even rimmed, without operculum, with or without diaphragm, pedicellate or sessile, adnate in some species ; hydranth with conical hypostome ; gonothecae aggregated as scapus or coppinia ; sexual generation a fixed sporosac.

TYPE GENUS. *Lafoea* Lamouroux, 1821.

REMARKS. Naumov (1960, 1969) has proposed two sub-families, diagnosed as follows :

Subfamily EULAFOEINAE. Lafoeidae lacking hydrothecal diaphragm ; gonosome in form of coppinia (type-genus *Lafoea* Lamouroux, 1821).

Subfamily LICTORELLINAE. Lafoeidae with hydrothecal diaphragm ; gonosome in form of scapus (type-genus *Lictorella* Allman, 1888). In the present area only the first subfamily is represented.¹

Sub-family **EULAFOEINAE** Naumov, 1960

With the characters discussed immediately above.

Genus **FILELLUM** Hincks, 1868

Campanularia : Hassall, 1848 : 2223.

Capsularia : Gray, 1848 : 151 (part) ; Naumov, 1960 : 280 ; Naumov, 1969 : 303 ; [non *Capsularia* Cuvier, 1797 : 665 (= *Coryne* Gaertner, in Pallas, 1774) (Lamouroux, Saint-Vincent & Deslongchamps, 1824 : 224) ; Gray, 1848 : 88 (= *Lafoea* Lamouroux, 1821) ; see Remarks].

Reticularia Thomson, 1853 : 443 ; Rees & Thursfield, 1965 : 85 (part).

Filellum Hincks, 1868 : 214 [nom. nov. pro *Capsularia* : Gray, 1848 (part)] ; Vervoort, 1972 : 50.

Grammaria : Vervoort, 1946 : 194 (part).

DIAGNOSIS. Colony comprising a creeping, irregularly-branched stolon bearing hydrothecae without pedicels. Hydrothecae tubular, curved centrally, without operculum. Gonothecae borne in hermaphrodite coppiniae typical of the sub-family.

TYPE SPECIES. *Campanularia serpens* Hassall, 1848 (Hincks, 1868, by monotypy ; Naumov, 1960 : 280 ; Naumov, 1969 : 303).

REMARKS. The genus *Capsularia* Cuvier, 1797, was considered by Naumov (1960, 1969) to be identical with *Filellum* Hincks, 1868. This seems unlikely, however, since Cuvier stated that the hydranths in *Capsularia* were non-retractile. *Capsularia* was referred to *Coryne* Gaertner, in Pallas, 1774, by Lamouroux, Saint-Vincent and Deslongchamps (1824 : 220), and this synonymy was discussed and accepted by Bedot (1901 : 437). Gray (1848 : 61) also included *Capsularia* in the synonymy of *Coryne*, but elsewhere in the same work (pp. 85–88, 151) used the name for species now included in other genera and also (p. 151) for the generic name of the species here called *Filellum serpens* (Hassall, 1848).

Vervoort (1972 : 50) showed the name *Reticularia* Thomson, 1853, to be preoccupied by the brachiopod name *Reticularia* McCoy, in Griffith, 1844.

Filellum serpens (Hassall, 1848)

(Fig. 2)

Campanularia serpens Hassall, 1848 : 2223 ; Hassall & Coppin, 1852 : 163, pl. 21, fig. 4.

Capsularia serpens : Gray, 1848 : 151.

Reticularia immersa Thomson, 1853 : 443, pl. 16a, figs 2–3.

¹ The species *Zygophylax pinnata* (Sars, 1874), from the second sub-family, has yet to be recorded from the area and appears seldom to occur within Continental Shelf depths in Europe. Although Kramp (1935) suggested the species might occur in northern Danish waters there are apparently still no records (K. W. Petersen, pers. comm.). It has, however, been recorded from a depth of 90 m in Hardanger Fjord, W Norway (Broch, 1918) and from N Biscay at 186 m depth (Billard, 1923). A statement that the species occurs along 'the entire coast of Europe from [the] Bay of Biscay' northwards (Naumov, 1969) seems erroneous.

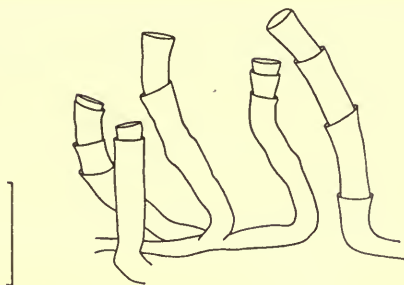


FIG. 2. *Filellum serpens*. Part of colony, W Scotland (1967.11.10.5). Scale = 500 μ m.

Filellum serpens: Hincks, 1868: 214–215, pl. 41, fig. 4 (syn. *Reticularia immersa* Thomson); Naumov, 1960: 281, figs 47, 170, 171; Naumov, 1969: 303, figs 47, 170, 171; Vervoort, 1972: 49–50.

Lafoea abietina: Billard, 1904: 164 (see Remarks).

Grammaria serpens: Vervoort, 1946: 194–196, fig. 82.

Reticularia serpens: Rees & Thursfield, 1965: 87–88.

TYPE MATERIAL. Holotype: Dublin, 1842, infertile colony on herbarium specimen of *Abietinaria abietina* (Linnaeus, 1758), coll. A. H. Hassall, 1973.10.8.4; mentioned Gray, 1848: 151.

OTHER MATERIAL EXAMINED. Vattlestraumen, Espegrend, nr Bergen, Norway, 30–40 m, 15 Aug. 1962, colony on *Abietinaria abietina*, infertile fragments in spirit and coppinia on microslide, coll. W. J. Rees, 1962.11.7.10. Väderö Islands, Sweden, 1 Oct. 1964, colony teased from substrate, on microslide, coll. W. J. Rees, 1967.11.10.6. Gåsö Ranna, Gullmarfjord, Sweden, 20–30 m, infertile colony on *Abietinaria abietina*, in spirit and on microslide, coll. W. J. Rees, 1962.11.8.14. Newhaven, nr Leith, Edinburgh, Scotland, infertile colony on *Abietinaria abietina*, dried material, holotype of *Reticularia immersa* Thomson, 1853, 1922.6.19.6. Off Millport, Great Cumbrae Island, Bute, Scotland, 40 m, infertile colonies on *Kirchenpaueria pinnata* (Linnaeus, 1758) and *Nemertesia ramosa* (Lamarck, 1816), 10 Sep. 1970, coll. C. Edwards, 1971.5.11.33. Off lighthouse, Little Cumbrae Island, 31 Jul. 1966, infertile colony on unidentified substrate, microslide, coll. W. J. Rees, 1967.11.10.5 (Fig. 2). 'Ireland', 13 Jan. 1902, infertile colony on *Abietinaria abietina*, microslide, coll. E. T. Browne, 1959.9.17.119. False Bay, Republic of South Africa, fertile colony on *Amphisbetia operculata* (Linnaeus, 1758), spirit, coll. N. A. H. Millard, 1957.4.26.37 (mentioned Millard, 1957: 203).

DESCRIPTION. Colony stolonal, tortuous; branching frequent and irregular with hydrothecae at irregular intervals. Hydrothecae tubular, wider than stolons, bent upwards at 60–90° approximately in centre; rim even, sometimes flared, without operculum; renovations frequent; basal $\frac{1}{4}$ – $\frac{2}{3}$ of hydrotheca adnate, narrower (Naumov, 1960, 1969), wider (Vervoort, 1972) or same width as upper part. Hydrothecae more or less spaced out depending on amount of substrate available (Hincks, 1868). Hydranth greenish (Hincks, 1868) or lemon-yellow (Hamond, 1957);

tubular, with conical hypostome; 9-12 tentacles, alternately elevated and depressed. Gonothecae borne in hermaphrodite coppiniae typical of the sub-family.

MEASUREMENTS. See Table 1.

TABLE I
Filellum serpens. Measurements in μm

	E SCOTLAND (holotype of <i>R. immersa</i> Thomson)	W SCOTLAND (1967.11.10.5)	IRELAND (1959.9.17.119)	NORWAY (1962.11.7.10)
HYDROTHECA				
Diameter at rim	90-140	100-175	115-135	—
Length of free part	—	200-900	80-170	—
Length of attached part	—	200-300	220-300	—
HYDRORHIZA				
Diameter of stolon	60*	100	100	—
COPPINIA (young)				
Overall length	—	—	—	c. 1500
Overall width	—	—	—	c. 1000

* Dried material.

VARIATIONS. Hydrothecae in this species are longer in some specimens than in others, long hydrothecae usually being those with one or more renovations. The hydrothecal rim appears to be flared in some specimens and simply tubular in others, with intermediate conditions. The angle at which the distal portion of the hydrotheca is raised varies approximately between 60° and 90° . The proportion of the hydrotheca which is adnate varies between $\frac{1}{4}$ and $\frac{2}{3}$ of the total length. Hydrothecae may be either narrower (Naumov, 1960, 1969) or wider (Vervoort, 1972) basally than distally, or of uniform diameter. Hydranth colour has been recorded as greenish (Hincks, 1868) and lemon yellow (Hamond, 1957). Colonies growing in a limited space – as on another hydroid colony – have the hydrothecae closer spaced than in colonies with ample substrate – as on a bivalve shell (Hincks, 1868).

REPRODUCTIVE SEASON. Fertile material recorded April–August off Norfolk (Hamond, 1957), April off NW France (Teissier, 1965), mid August off Norway (1962.11.7.10).

DISTRIBUTION. Common throughout the area.

HABITAT. Sublittoral to edge of continental shelf; apparently not recorded intertidally. Recorded growing most frequently on sertularian hydroids, especially *Abietinaria abietina*, but also *Hydrallmania falcata* (Linnaeus, 1758) and *Sertularia cupressina* Linnaeus, 1758. Also occurs on non-living substrates such as bivalve shells. Hincks' (1868) statement that the species is parasitic almost certainly referred to the growth of the species over other hydroids, and was probably not intended to imply an association of living tissues.

REMARKS. Many authors have considered the two nominal species *Filellum serpens* (Hassall, 1848) and *Reticularia immersa* Thomson, 1853, to be conspecific and the present examination of type material of both species supports this view.

The material recorded by Billard (1904 : 164) from Cherbourg as *Lafoea abietina* is here identified as *Filellum serpens*. The specimen was a lafoeid growing over a colony of a sertularian hydroid, *Abietinaria abietina*. Billard stated that it resembled a colony of *F. serpens* except that the hydrothecal aperture was not flared (*élargie*), and hence concluded that the specimen was a stoloniferous growth of *Grammaria abietina*. Such colony habit has not otherwise been recorded from *G. abietina*, and it is now known (present paper) that hydrothecae of *F. serpens* are not invariably flared. *G. abietina* is, therefore, unrecorded from the English Channel (see p. 384).

Genus **GRAMMARIA** Stimpson, 1854

Grammaria Stimpson, 1854 : 9 ; Broch, 1918 : 18 ; Totton, 1930 : 161 ; Vervoort, 1946 : 194 (part) ; Naumov, 1960 : 283 ; Vervoort, 1972 : 56.

Salacia : Hincks, 1868 : 211 ; [non *Salacia* Lamouroux, 1816 : 212 ; Stechow, 1922 : 150 ; Rees & Thursfield, 1965 : 149 ; = *Thuiaria* Fleming, 1828 (see Remarks)].

Reticularia : Rees & Thursfield, 1965 : 85 (part).

TYPE SPECIES. *Grammaria robusta* Stimpson, 1854 (= *Campanularia abietina* Sars, 1850 ; by designation by Totton, 1930).

DIAGNOSIS. Hydrocaulus polysiphonic, branched ; hydrothecae tubular, outward-curving, even-rimmed, lacking operculum and diaphragm, arranged in longitudinal rows ; with hermaphrodite coppiniae.

REMARKS. The name *Salacia* Lamouroux, 1816, was used for the present genus by Hincks (1868). The type species of *Salacia* is *S. tetracythara* Lamouroux, 1816² (by monotypy). The type material was examined by Deslongchamps (in Lamouroux, Saint-Vincent & Deslongchamps, 1824) who criticized Lamouroux' description as inaccurate and commented that the vase-shaped gonotheca of the specimen, shown clearly in the original illustration, suggested its affinities were with the genus *Sertularia* Linnaeus, 1758. Later Bale (1884) examined the same specimen and referred it to *Thuiaria* Fleming, 1828. Bale also provided a new trivial name, calling the species *Thuiaria fenestrata*. Like Deslongchamps, Bale considered Lamouroux' description to be inaccurate and, somewhat illogically, regarded *Salacia* as unavailable. In this he was followed by Bedot (1901), who did not see the specimen. Billard (1909) did see the specimen and confirmed that it had the characters of the genus *Thuiaria* which name he employed although it was junior to *Salacia*. Stechow (1922, 1923) seems to have been the first to have included *Thuiaria* in the synonymy of *Salacia*, his usage being followed by Rees & Thursfield (1965). Unfortunately the type material of *Salacia tetracythara* was destroyed along with the bulk of the Lamouroux collection at Caen by a bomb on 7 July 1944 (Redier, 1967), but there would seem little doubt from the available evidence that *Salacia* is a senior synonym of *Thuiaria*. Hincks (1868) thus seems to have been unjustified in including the genus *Grammaria* Stimpson, 1854, in the synonymy of *Salacia*. The earliest available name for the present genus is thus *Grammaria*.

Totton (1930 : 161) nominated *G. robusta* Stimpson, 1854, as genotype. It appears to be conspecific with *G. abietina* (Sars, 1850).

² Various subsequent authors have spelt the specific name *tetracythara*.

Vervoort (1946) and Rees & Thursfield (1965) regarded as congeneric the two genera here called *Grammaria* and *Filellum*. The distinction adopted here, however, follows Vervoort's more recent opinion (1972) that colony habit is of generic value. Nevertheless further information on the life-cycles of the species concerned and of other species of Lafoeidae may show this generic distinction to be inappropriate.

***Grammaria abietina* (Sars, 1850)**

(Fig. 3)

Campanularia abietina Sars, 1850 : 139.

Grammaria robusta Stimpson, 1854 : 9, pl. 3, fig. 1.

Grammaria ramosa Alder, 1856 : 361-362, pl. 14, figs 1-4.

Salacia abietina : Hincks, 1868 : 212-213, pl. 41, fig. 3 (syn. *G. robusta* Stimpson).

Grammaria stentor Allman, 1888 : 48, pl. 23, figs 1, 1a ; Hartlaub, 1905 : 599-600, fig. V² (syn. *G. intermedia* Pfeffer) ; Jaderholm, 1905 : 22-23, pl. 8, figs 4-5 (syn. *G. intermedia* Pfeffer) (syn. nov.) ; [? non *Grammaria stentor* : Linko, 1911 : 140-143, fig. 23 ; Naumov, 1960 : 282-283, fig. 173 ; Naumov, 1969 : 305-306, fig. 173 ; (see Remarks)] ; (syn. nov.).

Grammaria magellanica Allman, 1888 : 48-49, pl. 23, figs 2, 2a-b ; Vervoort, 1972 : 58-60, fig. 166 ; (syn. nov.).

Grammaria insignis Allman, 1888 : 49, pl. 23, figs 3, 2a-b ; (syn. nov.).

Grammaria intermedia Pfeffer, 1889 : 53-54.

Grammaria abietina : Broch, 1917 : 1-16, figs A-C, pls 1-2 ; Broch, 1918 : 18-21 ; Kramp, 1935 : 127-128, fig. 55 ; Naumov, 1960 : 283-284, fig. 174 ; Naumov, 1969 : 306-307, fig. 174 ; Calder, 1970 : 1523, pl. 5, fig. 1 ; Vervoort, 1972 : 56 (syn. *G. robusta* Stimpson).

Grammaria abietina var. *brevicyatha* Broch, 1918 : 20-21, fig. 5.

Reticularia abietina : Rees & Thursfield, 1965 : 85-86 (syn. *G. robusta* Stimpson).

TYPE MATERIAL AND LOCALITY. Colony 25 mm high, near Bergen, Norway, 55-75 m, summer of 1849 (Sars, 1850) ; specimen not located.

MATERIAL EXAMINED.³ *North Atlantic* : Carl Island and Cape Torell, Spitzbergen, colony in spirit, coll. A. E. Eaton, 1874.4.4.59a. Unnamed locality, Spitzbergen, fragments of colonies in spirit, coll. A. E. Eaton, 1874.4.4.64. E of Faroes, 62°01' N, 5°19' W, 210 m, 1869, two colonies in spirit, coll. H.M.S. 'Porcupine', via A. M. Norman coll., 1912.12.21.303. Trondheim Fjord, Norway, 1893, fragments of hydrocauli in spirit and 1 microslide (Fig. 3), via A. M. Norman coll., 1912.12.21.599. Brattholmen, Hjeltefjord, Espegrend, nr Bergen, Norway, 40-90 m, 9 Apr. 1962, infertile part of colony in spirit and one coppinia on microslide, coll. W. J. Rees, 1962.10.7.23. Off Huglin, Hardanger Fjord, Norway, 180 m, 1879, several colonies in spirit, via A. M. Norman coll., 1912.12.21.305. Shetland Isles, 1861, several colonies in spirit, coll. A. M. Norman, 1912.12.21.302. Northumberland coast, branched colony on herbarium sheet, coll. J. Alder, Hancock Museum, Newcastle-upon-Tyne [syntype of *Grammaria ramosa* Alder, 1856 ; figured, Alder, 1856 : pl. 14, fig. 1 (J. B. Garfath, pers. comm.)]. Dried colony in glass tube, Northumberland coast, coll. J. Alder, 1857.8.3.52 [syntype of *Grammaria ramosa* Alder, 1856]. Northumberland, branched hydrocaulus in spirit, coll. J. Alder, via A. M. Norman coll., 1912.12.21.301 (? mentioned, Hincks, 1868 : 213).

³ With the exception of 1962.10.7.23 all material listed is infertile.

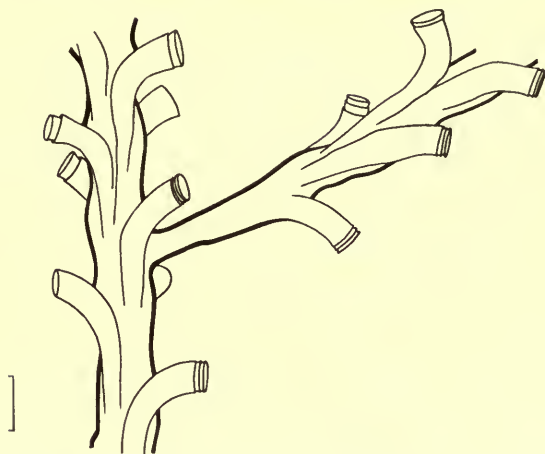


FIG. 3. *Grammaria abietina*. Part of colony, Trondheim Fjord, Norway (1912.12.21.599).
Scale = 500 μ m.

NE of Shetland Isles, $61^{\circ}35' N$, $0^{\circ}47' E$ ('Goldseeker' sta. 10), 204 m, 3 Sept. 1908, two fragments of hydrocauli on microslide, via J. Ritchie coll., 1964.8.7.61 (mentioned, Rees & Thursfield, 1965 : 85). *Other areas*: Barents Sea, 'Vitiáz' sta. 523, 110 m, 16 Aug. 1950, large colony in spirit, Leningrad Academy of Sciences Zoological Museum, and microslide donated to British Museum (Natural History), 1975.7.11.1 (mentioned as *G. stentor* Allman, Naumov, 1960 : 283 ; 1969 : 306 ; see Remarks). Near Falkland Islands, $51^{\circ}35' S$, $65^{\circ}39' W$, 130 m ('Challenger' sta. 314), 21 Jan. 1876, two branched fragments of colonies plus one microslide, coll. H.M.S. 'Challenger', 1888.11.13.36 (syntypes of *Grammaria magellanica* Allman, 1888). Royal Sound, Kerguelen Island, $49^{\circ}28' S$, $70^{\circ}13' E$, 37–110 m ('Challenger' sta. 149D), 20 Jan. 1874, fragments of colonies in spirit plus one microslide, coll. H.M.S. 'Challenger', 1888.11.13.35 (syntypes of *Grammaria stentor* Allman, 1888). Off Marion Island, S Indian Ocean, $46^{\circ}43' S$, $38^{\circ}04' E$, 90–135 m ('Challenger' sta. 145), 27 Dec. 1873, colony and fragments in spirit plus one microslide, coll. H.M.S. 'Challenger', 1888.11.13.37 (syntypes of *Grammaria insignis* Allman, 1888).

DESCRIPTION. Colony erect, main stem and branches polysiphonic, branching irregular or imperfectly pinnate, branches tapering near the base. Hydrothecae long, tubular, variably outward-curving ; rims even, circular, often renovated, frequently slightly flared ; no apparent junction with pedicel ; arranged in 4–8 longitudinal rows with hydrothecae of adjacent rows alternate ; if 4 rows, hydrothecae often in decussate pairs. Hydranth yellow (Hincks, 1868), extensible roughly one hydrotheca-length beyond aperture ; widest distally, hypostome conical, 18–20 tentacles held alternately elevated and depressed. Gonothecae borne in hermaphrodite coppinae 'arranged on branches in small muffs. Surface of coppinia smooth owing to dense arrangement of the sterile tubes, their inwardly-curved ends forming a thick protective tangle above the gonothecal mouths' (Naumov, 1969).

MEASUREMENTS. See Table 2.

TABLE 2

Grammaria abietina. Measurements in μm

	NORTH SEA (1964.8.7.61)	TRONDHEIM FJORD (1912.12.21.599)	NR BERGEN, NORWAY (1962.10.7.23)
HYDROTHECA			
Diameter at rim	240-280	280-360	280-490
COPPINIA			
Overall length	—	—	3000
Overall width	—	—	1500
Diameter of sterile tubes	—	—	90-130

VARIATION. There are normally 4, 5 or 6 rows of hydrothecae on a hydrocaulus, and 8 rows have been recorded (Vervoort, 1972, as *G. magellanica*). When in 4 rows the hydrothecae are in opposite or almost opposite pairs. The hydrothecal rim is flared in some specimens and straight in others, this character having apparently no systematic value. The degree of outward curving of the hydrotheca varies, so that the plane of the hydrothecal aperture is parallel with the axis of the hydrocaulus in some specimens, while in specimens with shorter hydrothecae the plane of the aperture makes an angle of about 45° with the axis, and this character may vary even within a colony (Fig. 3).

REPRODUCTIVE SEASON. Little information. Fertile specimen taken near Bergen, Norway, 9 Apr. 1962 (1962.10.7.23).

DISTRIBUTION. Widely distributed in sub-arctic and arctic areas (Broch, 1918), extending south to much of the North Sea and some Danish waters. There seems to be no valid record from western coasts south of the Shetlands. Southerly records include Northumberland (Hincks, 1868; present material), Skagerrak (Kramp, 1935) and Oslo Fjord (Christiansen, 1972). A record from the north coast of France (Billard, 1904, repeated in Broch, 1918) is probably erroneous (see p. 381) and the statement of Christiansen (1972) that the species occurs on that coast lacks evidence. The weight of published opinion is that the species is absent from the English Channel and southern North Sea (Hincks, 1868; Hartlaub, 1895; Broch, 1927; Vervoort, 1946, 1949; Leloup, 1952; Hamond, 1957; Marine Biological Association, 1957; Teissier, 1965; Robins, 1969).

HABITAT. Published records indicate that the normal depth-range of this species is approximately 50-1500 m in boreal waters, rising to 10-250 m in arctic regions (Linko, 1911; Naumov, 1960, 1969; Christiansen, 1972). The species has been recorded on both silty and rocky substrates (Naumov, 1960, 1969; Calder, 1970).

REMARKS. There seems no doubt from the original description of *Grammaria ramosa* Alder, 1856, that it should be regarded as a junior synonym of the present species and examination of the type series confirms that they are conspecific.

Vervoort (1972) has expressed doubt as to the distinctiveness of the three species erected by Allman (1888), *Grammaria insignis*, *G. magellanica* and *G. stentor*, and following examination of the type material they are here referred to the present

species. The characters on which they were based were differences in the branching of the colony and of the number of rows of hydrothecae, and whether or not the hydrothecal rim was flared. These characters are now known to be variable in *G. abietina* and the three species proposed by Allman appear invalid.

The material assigned to *G. stentor* Allman, 1888, by Linko (1911) and Naumov (1960, 1969, examined here) has hydrothecae longer than in *G. abietina* as here defined, and may represent a distinct species. If so, a new name will have to be provided. *G. stentor* sensu Hartlaub, 1905, and Jaderholm, 1905, fall within the proposed limits of *G. abietina*. Jaderholm examined the type material of *G. intermedia* Pfeffer, 1889, and referred it to his own concept of *G. stentor*. His account suggests that *G. intermedia* also should be referred to *G. abietina*.

G. abietina var *brevicyatha* Broch, 1818, was distinguished on the basis of short, slightly out-turned hydrothecae, but such variation seems normal for the species and no distinct variety need be recognized.

The material from Cherbourg, N France, referred to the present species by Billard (1904 : 164) is here identified as *Filellum serpens* (see p. 381).

Genus *LAFOEA* Lamouroux, 1821

Sertularia : Fleming, 1820 : 83 (part).

Lafoea Lamouroux, 1821 : 8 ; Hincks, 1868 : 198 (part) ; Naumov, 1960 : 272 ; Naumov, 1969 : 295.

NOMENCLATURE. The genus was named after an amateur botanist, Professor de Lafoye, of the University of Caen (Lamouroux, 1821 ; Lamouroux, Saint-Vincent & Deslongchamps, 1824).

TYPE SPECIES AND MATERIAL. *Lafoea cornuta* Lamouroux, 1821 : 8, pl. 65, figs 12-14 (by monotypy) ; 44-44½° N, 52-53° W, 55-60 m ; branched colony 100 mm long, coll. Capt. Laporte (Lamouroux, 1821) ; Botanical Institute collections, Caen. Specimen destroyed by bomb, 7 July 1944 (Redier, 1967).

DIAGNOSIS. Colony either stoloniferous or with stolons united to form erect polysiphonic hydrocauli with monosiphonic terminal branches. Hydrothecae lacking both operculum and diaphragm ; tubular or bell-shaped, sometimes bent and thus bilaterally symmetrical ; rim even, circular, sometimes flared ; renovations frequent ; pedicel twisted if present ; gonothecae borne in hermaphrodite coppinae.

REMARKS. Billard (1909 : 311) examined the genotype material and referred the type species *L. cornuta* Lamouroux, 1821, to *L. dumosa* (Fleming, 1820), supporting the suggestion of Hincks (1868 : 199) that the two are conspecific.

Lafoea dumosa (Fleming, 1820)

(Fig. 4)

Sertularia dumosa Fleming, 1820 : 83-84.

Lafoea cornuta Lamouroux, 1821 : 8, pl. 65, figs 12-14.

Campanularia dumosa : Fleming, 1828 : 548-549 ; Johnston, 1832 : 254, pl. 11, fig. 11 ; Johnston, 1838 : 157, pl. 23, figs 2-5 ; Johnston, 1847 : 113-115, pl. 27, figs 2-5, text-figs 20-21.

Capsularia dumosa: Gray, 1848: 88.

Campanularia fruticosa Sars, 1850: 138-139; (syn. nov.).

Campanularia gracillima Alder, 1856: 361, pl. 14, figs 5-6.

Lafoea dumosa: Hincks, 1868: 200-201, pl. 41, fig. 1, 1a (? syn. *L. cornuta* Lamouroux); Nutting, 1899: 747-751, pl. 64; Rufford, 1902: 62; Billard, 1909: 311 (syn. *L. cornuta* Lamouroux); Broch, 1918: 7-9; Totton, 1930: 158, fig. 14; Kramp, 1935: 123-124, figs 52a, 53; Fraser, 1944: 221-222, pls 45-46, fig. 205a-e; Ralph, 1958: 310; Rees & Thursfield, 1965: 79-80; Teissier, 1965: 19; Calder, 1970: 1524, pl. 5, fig. 3.

Lafoea fruticosa: Hincks, 1868: 202-203, pl. 41, figs 2, 2a-b (syn. *C. gracillima* Alder); Broch, 1918: 12-15 (syn. *L. pocillum* Hincks); Totton, 1930: 157-158, fig. 13; Kramp, 1935: 124-125, fig. 52c-d (syn. *L. pocillum* Hincks); Fraser, 1944: 223-224, pl. 46, fig. 206; Hodgson, 1950: 11; Naumov, 1960: 275-276, fig. 164; Millard, 1964: 13-14, fig. 3a-f; Rees & Thursfield, 1965: 80 (syn. *L. pocillum* Hincks); Millard, 1967: 175-176, fig. 2c; Naumov, 1969: 297-298, fig. 164; Calder, 1970: 1524-1525, pl. 5, fig. 4; Vervoort, 1972: 66-74, figs 19-21 (syn. *L. gracillima* Alder).

Lafoea pocillum Hincks, 1868: 204, pl. 40, fig. 2; Hincks, 1874b: 147; Crawford, 1895: 260; Rufford, 1902: 62; Linko, 1911: 114-116, fig. 20; Naumov, 1960: 273-274, fig. 161 (syn. *Campanularia parvula* Hincks); Naumov, 1969: 295-296, fig. 161 (syn. *C. parvula* Hincks).

Hebella pocillum: Ritchie, 1911: 33.

Lafoea gracillima: Broch, 1918: 9-11; Totton, 1930: 158-159, fig. 15a-b; Kramp, 1935: 125, fig. 52b; Fraser, 1944: 224-225, pl. 46, fig. 207; Ralph, 1958: 310, figs 1y, 2a-c; Rees & Thursfield, 1965: 80-81; Teissier, 1965: 20; Calder, 1970: 1525, pl. 5, fig. 5.

Lafoea fruticosa forma *pocillum*: Vervoort, 1949: 148-149.

TYPE MATERIAL. Arbroath, Angus, Scotland, 1809;⁴ location of specimens unknown.

MATERIAL EXAMINED. Brattholmen, Hjeltefjord, nr Bergen, Norway, 40-90 m, 9 Apr. 1962, part of a colony on microslide, coll. W. J. Rees, 1962.10.7.22 (Fig. 4). Kosterfjord, Sweden, 58°50' N, 11°00' E, 80-100 m, 23 Sep. 1964, hydrocaulus on microslide, coll. W. J. Rees, 1965.1.14.73. Väderö Islands, Sweden, 58°05' N, 11°04' E, 80 m, 1 Oct. 1964, several colonies in spirit, coll. W. J. Rees, 1965.1.14.136 and 1966.1.4.65. Löken, Gåsö Ranna, Gullmarfjord, Sweden, 25-30 m, 14 May 1959, two fertile colonies on *Abietinaria* sp., in spirit, coll. W. J. Rees, 1959.6.11.36. Gåsö, Gullmarfjord, Sweden, 20-30 m, 27 Aug. 1962, hydrocaulus on microslide, coll. W. J. Rees, 1962.11.8.13. Off Balta, Shetland Isles, Scotland, 100 m, colony in spirit, coll. A. M. Norman, 1912.12.21.237. Oban, Argyll, Scotland, two hydrocauli on microslide and colony on herbarium sheet, coll. T. Hincks, 1899.5.1.160, 216. Oban, Argyll, Scotland, infertile colony on *Phycodrys rubens* (L.) Batt.,⁵ in spirit, 1899.5.1.162 (holotype of *Lafoea pocillum* Hincks, 1868). Off Millport, Great Cumbrae Island, Bute, Scotland, 40 m, 18 Sep. 1970, four colonies in spirit, coll. C. Edwards, 1971.5.11.31. Berwick Bay, Berwickshire, Scotland, and Northumberland, England, several colonies on four herbarium sheets, coll. G. Johnston, 1847.9.24.68, 69, 70, 71 (mentioned, Gray, 1848: 88; ? Johnston, 1838: 157). 'Deep water, Northumberland' (label with specimen), colony on herbarium sheet, coll. J. Alder, Hancock Museum, Newcastle-upon-Tyne [paratype of

⁴ Fleming (1820) based the original description on specimens from three Scottish localities: from refuse of oyster-boats, 'Newhaven', identified in a later work as being near Edinburgh (Fleming, 1828); 'Aberbrothick', now called Arbroath, Angus; and 'Zetland'. The first and last being relatively imprecise, the type locality is here restricted to Arbroath.

⁵ Det. J. M. Price.

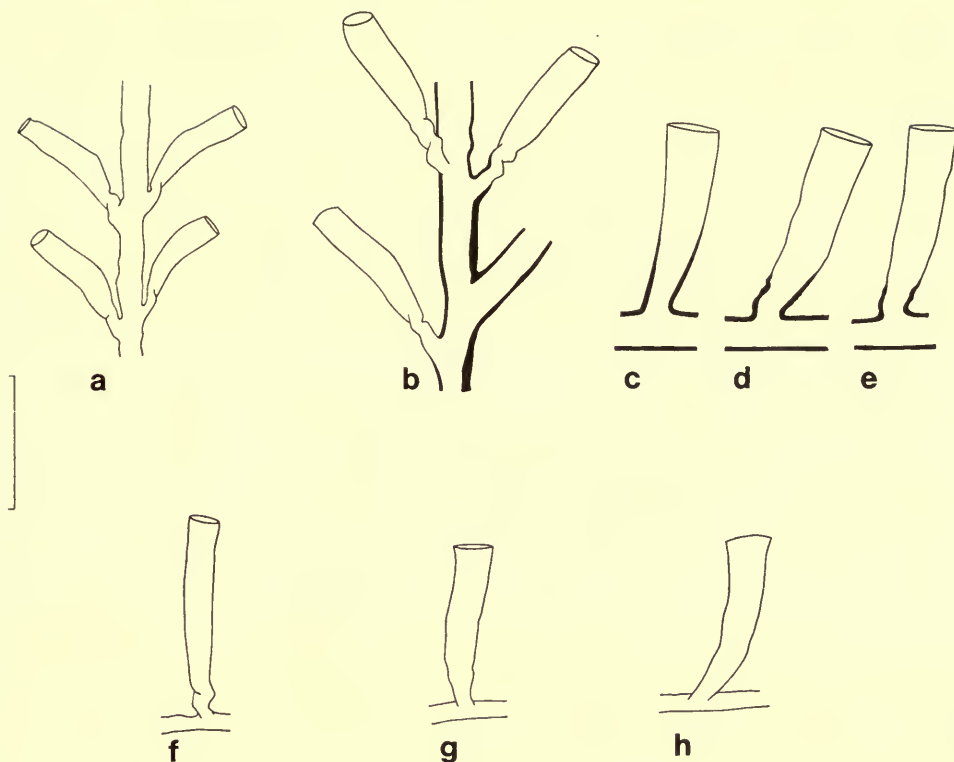


FIG. 4. a-e, *Lafoea dumosa*. a, part of colony, near Bergen, Norway, 40-90 m (1962.10.7.22); b, part of colony, east of Straits of Magellan, Argentina, 100 m (1890.4.11.2d); c-e, three adjacent hydrothecae, SW England (1959.9.17.108). f-h, three hydrothecae of holotype of *Lafoea pocillum* (1899.5.1.162), here referred to *L. dumosa*. Scale (a-h) = 500 μ m.

Campanularia gracillima Alder, 1856; figured specimen, Alder, 1856: pl. 14, fig. 5 (J. B. Garfath, pers. comm.). Probably off Northumberland, 'in deep water' (Alder, 1856), colony in spirit, coll. J. Alder, 1857.8.3.51 [lectotype of *Campanularia gracillima* Alder, 1856 (Totton, 1930)]. Scarborough, Yorkshire, England, colonies on two herbarium sheets (one on *Flustra* sp.) coll. W. Bean, via G. Johnston coll., 1842.12.9.1, 1847.9.24.67 (mentioned, Gray, 1848: 88). North Sea, 60°02' N, 3°13' W, 160 m, 19 June 1906 ('Goldseeker' sta. 21a), two hydrocauli on microslide, coll. J. Ritchie, 1964.8.7.54 (mentioned, Rees & Thursfield, 1965: 80). North Sea, 59°21' N, 5°00' W, 125 m, 6 July 1906 ('Goldseeker' sta. 50), hydrocaulus on microslide, coll. J. Ritchie, 1964.8.7.50 (mentioned, Rees & Thursfield, 1965: 81). Plymouth, Devon, 8 Mar. 1898, hydrocauli on two microslides, coll. E. T. Browne, 1959.9.17.108, 114. Eddystone Ground, NW English Channel, 8 Mar. 1898, seven hydrocauli on microslide, coll. E. T. Browne, 1959.9.17.111. Eddystone ground, NW English Channel, 30 Mar. 1938, hydrocaulus on microslide, coll. W. J. Rees,

1969.12.2.45. Probably British, two colonies on herbarium sheets, coll. G. Johnston, 1847.9.24.69, 72 (mentioned, Gray, 1848 : 88).

Davis Strait, Greenland, 66°59' N, 55°27' W, 120 m, fragments of hydrocaulus on microslide, coll. H.M.S. 'Valorous', 1878.3.26.3. E of Str. of Magellan, Argentina, 52°20' S, 67°39' W, 100 m, 20 Jan. 1876 ('Challenger' sta. 313), part of colony on microslide, coll. H.M.S. 'Challenger', 1890.4.11.2d (Fig. 4). Off Oates Land, Antarctic mainland, 69°43' S, 163°24' E, 329-366 m, 22 Feb. 1911 ('Terra Nova' sta. 194), spirit material and two microslides, coll. British Antarctic ('Terra Nova') Expedition, 1929.10.28.64 (mentioned, Totton, 1930 : 158).

DESCRIPTION. Colonies stoloniferous or erect. Stoloniferous colonies comprise irregularly-branched monosiphonic hydrorhizae with hydrothecae borne at irregular intervals. Erect colonies consist of polysiphonic hydrocauli, loosely and irregularly branched, arising from a straggling stolon network. Component perisarc tubes of erect colonies parallel, each bearing hydrothecae at irregular intervals giving bristly appearance. Hydrothecae long, tubular, even-rimmed, variably tapered below, sometimes asymmetrically; pedicel more or less well defined, usually kinked, but sometimes lacking so that hydrotheca is sessile. Form of hydrothecal pedicel usually constant within a colony. Hydranth long, retractile, *c.* 20 tentacles held alternately elevated and depressed (Kramp, 1935), hypostome conical. Hydranth and coenosarc often yellow. Gonothecae in hermaphrodite coppinae.

MEASUREMENTS. See Table 3.

TABLE 3

Lafaea dumosa. Measurements in μm

	W ENGLISH CHANNEL (1969.12.2.45)	W SWEDEN (1965.1.14.73)	N SCOTLAND (1964.8.7.50)	W SCOTLAND (1899.5.1.160)	W SCOTLAND (1899.5.1.162) (holotype of <i>Lafaea pocillum</i>)
HYDROTHECA					
Base to rim (unrenovated)	500-650	485-510	770-830	380-550	120-350
Diameter at rim	150-220	100	150-210	120-140	90-190
Pedicel length	0	100-150	50	140-170	80-170

VARIATION. The hydrothecal pedicel varies in length between colonies (see Remarks) and the degree of bilateral symmetry of the hydrothecae varies also. Neither character appears to be of systematic importance. Specimens from deep water have fewer hydrothecae per unit length of stolon, but within continental shelf depths this character seems constant. The so-called pedicel of the present species grades into the base of the hydrotheca. Although a pedicel is readily discernible if long, shorter pedicels are less distinct and it is possible to arrange specimens in a series in which the pedicel becomes progressively less distinct and is finally absent (Fig. 4). In each colony the range of pedicel length is small, but pedicellate hydrothecae can be found in colonies largely lacking pedicels, and sessile hydrothecae occur in predominantly pedicellate colonies.

REPRODUCTIVE SEASON. Fertile specimens recorded August in NW France (Teissier, 1965), 14 May 1959 in W Sweden (1959.6.11.36). The paucity of records suggests that in this species reproduction is usually vegetative.

DISTRIBUTION. Found throughout the area but apparently not common in the southern North Sea and eastern English Channel (Broch, 1918; Vervoort, 1946; Marine Biological Association, 1957; Teissier, 1965; Naumov, 1969), not having been found in a faunal survey off the coasts of Belgium (Leloup, 1952).

HABITAT. Occurs at all continental shelf depths, but not intertidally. On a wide variety of animal, plant and inert substrates, commonly on other hydroids; not on sand.

REMARKS. The two nominal species *Lafoea fruticosa* (Sars, 1850) and *L. gracillima* (Alder, 1856) have been regarded as conspecific by some authors (e.g. Hincks, 1868; Hodgson, 1950; Naumov, 1960, 1969; Millard, 1967; Vervoort, 1972) and as valid species by others (e.g. Broch, 1918; Kramp, 1935; Fraser, 1944; Rees & Thursfield, 1965; Calder, 1970). Vervoort's detailed appraisal is particularly convincing and his view that the two are conspecific is accepted here.

In contrast, it appears that the distinctness of *L. fruticosa* from *L. dumosa* has been questioned only by Millard (1964), who described intermediate material. The two species have been distinguished by Hincks (1868) and apparently all subsequent authors (except Rufford, 1902, and Ralph, 1958⁶) by the presence of a hydrothecal pedicel in *L. fruticosa* and its absence in *L. dumosa* which has been held to have sessile hydrothecae. However, the original description of *L. dumosa* (Fleming, 1820, repeated in Fleming, 1828) referred to 'nearly sessile' hydrothecae, implying that short pedicels were present. Johnston (1832) similarly mentioned 'nearly sessile' hydrothecae, stating that they 'can rarely be observed to be twisted at their insertions' as shown in his illustration. His later descriptions refer to 'nearly sessile' and 'almost sessile' hydrothecae (Johnston, 1838, 1847). Gray (1848) did not provide a description, but the ten colonies listed by him as *L. dumosa* and re-examined during the present work all have pedicellate hydrothecae. The material was from Johnston's collection, some being labelled Berwick Bay and probably, therefore, the Berwick Bay material described by Johnston (1832, 1838). Whether or not this is so it seems probable that Johnston, like Fleming, wished to imply that the pedicels were short, and not that they were absent. Further, in describing *L. gracillima*, Alder (1856) stated that the pedicels were 'longer' than in *L. dumosa*, indicating that he too considered *L. dumosa* to be pedicellate. Thus, when Hincks (1868) later gave specific status to specimens without pedicels and distinguished *L. fruticosa* as having them he was wrong to refer non-pedicellate material to *L. dumosa* and should have provided a new name. This seems never to have been done. It appears probable, however, that specimens lacking hydrothecal pedicels do not constitute a valid species and should nevertheless be referred to *L. dumosa* sensu Fleming, Johnston and Alder (op. cit.), *L. fruticosa* (Sars, 1851) and *L. gracillima* (Alder, 1856) falling within its synonymy.

⁶ In a key to the two taxa *L. dumosa* and *L. gracillima* Ralph separated them on the basis of short and long pedicels respectively, but she gave a description of *L. gracillima* only. Rufford ascribed a short pedicel to *L. dumosa* without comment.

The two nominal species *Lafoea parvula* (Hincks, 1853, as *Campanularia*) and *L. pocillum* Hincks, 1868, were thought to be conspecific by Naumov (1960, 1969). However, several authors (Broch, 1918; Kramp, 1935; Vervoort, 1949; Rees & Thursfield, 1965) have considered *L. pocillum* conspecific with *L. dumosa* (as *L. fruticosa*) and this opinion is supported by the present examination of the type material (Fig. 4). The material referred to *Hebella pocillum* (Hincks, 1868) by Fraser (1937, 1944) and Yamada (1955) is at present indeterminate; it may require a new specific name. The type material of *L. parvula* could not be located, but specimens labelled *L. parvula* (off Durham, England, coll. A. M. Norman, 1912.12.21.240) seemed identical with infertile colonies of *Calicella syringa* (Linnaeus, 1767) from which the hydrothecal operculae have been lost. It seems plausible that *L. parvula* was founded on such material.

Lafoea pygmaea Alder, in Hincks (1868: 205, pl. 40, fig. 3; type localities Tyne-mouth, Northumberland, and Sark, Channel Isles), was referred to *Calicella* in a later publication by Hincks [1874b: 147 (footnote)]. This was accepted by Jaderholm (1909: 80), Bedot (1912: 315), Broch (1918: 9) and Stechow (1921: 228). However, Kramp (1935: 125) and Vervoort (1946: 199) regarded *L. pygmaea* as identical with *L. gracillima* (= *L. dumosa*), while Naumov (1960, 1969) referred it to *L. pocillum* (= *L. dumosa*). The type material in the Hancock Museum, Newcastle-upon-Tyne, and the description of Hincks (1868: pl. 40, figs 3, 3a-b), showing a well-demarcated pedicel with transverse annulations, are clearly of *Calicella* and it seems Hincks was justified in placing *L. pygmaea* in that genus (Cornelius & Garfath, in prep.). *L. pygmaea* was regarded as conspecific with *C. syringa* (Linnaeus, 1767) by Jaderholm (1909) and Broch (1918).

Family **HALECIIDAE** Hincks, 1868

DIAGNOSIS. Colonial Hydroida with short, cylindrical hydrothecae usually wider than deep; hydrothecal rims even, often flared, renovation common, desmocytes large, often birefringent. Hydrothecal pedicel often lacking. Hydranths larger than hydrothecae. Gonothecae usually sexually dimorphic. Sexual generation said to be a medusa in *Campalecium* Torrey, 1902 (Kossowska, 1911), eumedusoid in *Hydranthea* Hincks, 1868, and a sessile sporosac in *Halecium* Oken, 1815, and *Ophiodissa* Stechow, 1919.

TYPE GENUS. *Halecium* Oken, 1815.⁷

REMARKS. The nature of the sexual generation was shown by Rees (1957) to be a valid generic character in only some families among the athecate capitate hydroids. In the Haleciidae it appears to be correlated with other generic characters and is included here in the generic diagnoses. A similar correlation has been shown in certain genera of the Campanulariidae (Cornelius, 1975).

⁷ Oken's book was placed on the list of rejected works by the International Commission on Zoological Nomenclature (1956: Opinion 417), but application is currently being made to the Commission for validation of the name *Halecium* (see Cornelius, 1976).

The small birefringent bodies found inside the hydrothecal wall throughout this family (Fig. 11) and widely referred to as punctae (e.g. Vervoort, 1972) are probably desmocytes. They resemble those previously described in other classes of coelenterates, reviewed by Chapman (1969), but are much larger, being visible in some species at only 20 diameters' magnification. A preliminary account of their ultrastructure is to appear elsewhere. It is probable that the 'punctae' of the family Lafoeidae are also desmocytes. Present knowledge suggests that they have little systematic value at species level in either family, but comparative studies of their ultrastructure might prove differently.

Genus *HALECIUM* Oken, 1815⁷

Halecium Oken, 1815: 91; Johnston, 1847: 58; Hincks, 1868: 220; Fraser, 1944: 183; Naumov, 1960: 442.

Thoa Lamouroux, 1816: 210; Johnston, 1838: 119.

Haloikema Bourne, 1890: 395.

TYPE SPECIES. *Sertularia halecina* Linnaeus, 1758: 809 (Oken, 1815: 91; Bedot, 1901: 448).

DIAGNOSIS. Haleciidae with branched, erect colonies; lacking nematophores, large nematocysts, medusae and eumedusoid gonophores. Gonothecae usually sexually dimorphic.

REMARKS. Johnston (1847) drew attention to the seniority of *Halecium* to *Thoa* and his synonymy was followed by Hincks (1868) and all subsequent authors. *Haloikema* was first included in *Halecium* by Bedot (1911).

Halecium torreyi Kossowska, 1911, said by that author to release a medusa, was placed in the synonymy of *Campalecium medusiferum* Torrey, 1902, by Huvé (1954).

Halecium beanii (Johnston, 1938)

(Fig. 5)

Thoa beanii Johnston, 1838: 120-121, pl. 7, figs 1-2.

Halecium beanii: Johnston, 1847: 59-60, pl. 9, figs 1-2; Hincks, 1868: 224-225, pl. 43, figs 2, 2a-c; Vervoort, 1946: 161-163, figs 65-66; Ralph, 1958: 332-334, fig. 10a-b, e-k; Rees & Thursfield, 1965: 105-106.

Halecium scutum Clarke, 1876: 14-15, pl. 4, figs 13-14.

Halecium boreale Lorenz, 1886: 26-27, pl. 1, figs 1-2.

Halecium beanei Stechow, 1919: 33 (lapsus pro *beanii*).

Halecium beani: Naumov, 1960: 447-449, fig. 336 (syn. *H. scutum* Clarke; *H. boreale* Lorenz); Naumov, 1969: 483-484, fig. 336.

NOMENCLATURE. The species is named after W. Bean, who collected the holotype.

TYPE MATERIAL AND LOCALITY. Holotype: Nr Scarborough, Yorkshire, England, in 'deep water', ♀ colony 42 mm high on herbarium sheet, plus one microslide of ♀ gonotheca from same colony, coll. W. Bean, 1847.9.18.181, 181a (Johnston, 1838, 1847).

⁷ See footnote on opposite page.

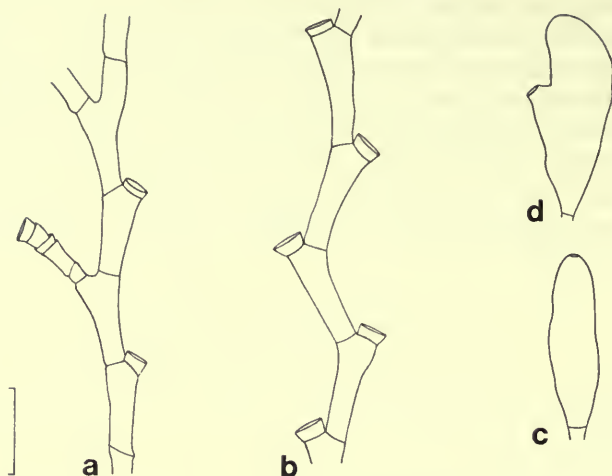


FIG. 5. *Halécium beanii*. a, part of colony, NE England (1956.2.2.27); b-c, part of colony and ♂ gonotheca, Isle of Man (1959.10.17.8); d, ♀ gonotheca, near Bergen, Norway (1962.11.7.38). Scale (a-d) = 500 μ m.

OTHER MATERIAL EXAMINED. Bergen Fjord, Norway, 30–80 m, 1878, two colonies in spirit, coll. A. M. Norman, 1912.12.21.191. Espeyrend, nr Bergen, Norway, 30 m, 9 Aug. 1962, ♀ colony on microslide, coll. W. J. Rees, 1962.11.7.38 (Fig. 5). NW of Bulbjerg, Denmark, 57° 12' N, 8° 54' E, 16 m, 3 Oct. 1922 ('Dana' sta. 2865), part of colony in spirit, coll. R. V. 'Dana', Copenhagen Zoological Museum (mentioned Kramp, 1935 : 50, as *Halécium articulatum*).

Off Durham, England, Jul. 1874, colony in spirit, coll. A. M. Norman, 1912.12.21.186. Filey, Yorkshire, ♀ colony in spirit, coll. T. Hincks, 1899.5.1.164. Bridlington Bay, Yorkshire, colony in spirit, coll. Ministry of Agriculture, Fisheries and Food, S.S. 'George Bligh', 1956.2.2.27 (Fig. 5). Sheerness, Kent, 10 Oct. 1892, one slide, coll. E. T. Browne, 1973.6.17.1. Weymouth Bay, Portland, Dorset, 20 m, several colonies in spirit, coll. R. Kirkpatrick, 1897.8.9.16. Berry Head, Brixham, Devon, 25 m, four ♀ colonies in spirit, coll. R. Kirkpatrick, 1893.8.7.3, 1897.8.9.16. Eddystone ground, off Plymouth, Devon, 15 Sep. 1897, several ♂ colonies on *Chaetopterus* tubes in spirit and one slide, coll. E. J. Allen, det. E. T. Browne, 1941.3.20.310. Plymouth, Devon, 1898, ♀ colony in spirit, coll. E. T. Browne, 1941.3.20.331. Isle of Man, 25 Mar. 1894, three colonies in spirit and one microslide (Fig. 5), coll. E. T. Browne, 1959.10.17.8.

DESCRIPTION. Colony erect, imperfectly pinnate, shrubby in habit. Main stem polysiphonic. Side-branches polysiphonic basally, component coenosarcs gradually branching off, final branches monosiphonic and usually flexuose; internodes equal, usually longer than broad, nodes oblique or transverse. Hydrothecae alternate, each on short hydrophore at distal end of internode; short, tubular, rim slightly flared, even. Usually 1–3 hydrothecal renovations, but up to 10 reported (Vervoort,

1972). Gonothecae on short pedicels below hydrothecae. ♂ club-shaped, aperture terminal; ♀ approximately bean-shaped, aperture tubular, in centre of concave side, c. 6 ova, 1 or 2 hydranths projecting through aperture.

MEASUREMENTS. See Table 4.

TABLE 4

Halecium beanii. Measurements in μm unless otherwise stated

	U.S.S.R. (Naumov, 1969)	NEW ZEALAND (Ralph, 1958)	SW ENGLAND (1959.9.17.3)	SE ENGLAND (1973.6.17.1)
HYDROTHERCA				
Length	50-70	60	20-25	25-45
Breadth at rim	200-250	—	115-150	110-140
HYDROCAULUS DIAMETER				
	—	120-180	120-180	120-150
LENGTH OF INTERNODES				
	—	250-750	250-700	500-530
♂ GONOTHECA				
Length	Up to 2200	620-1000	700-850	—
Breadth (max.)	—	250	120-180	—
♀ GONOTHECA				
Length	Up to 2200	1120-1125	—	1000-1200
Breadth (max.)	—	310	—	430-480
MAXIMUM HEIGHT OF COLONY				
	0.3 m	0.12 m	—	—

VARIATION. Hydrocauli of this species are variably flexuose; extremes are shown in Fig. 5.

REPRODUCTIVE SEASON. Fertile specimens recorded from S Devon, Norfolk and Roscoff, France, most months from January to October (Hamond, 1957; Marine Biological Association, 1957; Teissier, 1965).

DISTRIBUTION. Common throughout Britain and nearby seas. Apparently absent from the Baltic and rare in the Kattegat, commoner in the Skagerrak and Oslo Fjord (Broch, 1928; Christiansen, 1972).

HABITAT. Rocky substrates; 5-100 m depth, occasionally deeper.

Halecium halecinum (Linnaeus, 1758)

(Fig. 6)

Corallina scruposa pennata, *cauliculis crassiusculis rigidis* Ray, 1724: 36.

Corallina erecta, tubulosa, pennata, halecis spiniae facie Ellis, 1755: 17-19, pl. 10.

Sertularia halecina Linnaeus, 1758: 809.

Halecium halecinum: Oken, 1815: 91; Johnston, 1847: 58-59, pl. 8, figs 1-4; Hincks, 1868: 221-223, pl. 42, figs a-d; Broch, 1918: 36-38, fig. 11; Vervoort, 1946: 158-161, figs 63-64; Leloup, 1952: 140-141, fig. 74; Naumov, 1960: 446-447, fig. 335, pl. 17, fig. 3; Naumov, 1969: 482-483, fig. 335, pl. 17, fig. 3.

Thoa halecina: Johnston, 1838: 119-120, pl. 6, figs 1-4.

Halecium geniculatum Norman, 1867: 205; Hincks, 1868: 229; [non *Halecium geniculatum* Nutting, 1899 (= *H. tenellum* Hincks, 1861 (Naumov, 1960, 1969); see also synonymy of *H. tenellum*, p. 409)].

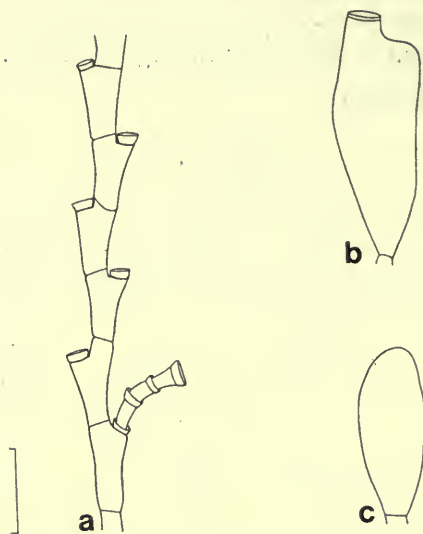


FIG. 6. *Halecium halecinum*. a-b, part of colony and ♀ gonotheca, Isle of Man (1959.9.17.5) ; c, ♂ gonotheca, SW England (1898.5.7.86). Scale (a-c) = 500 µm.

TYPE MATERIAL AND LOCALITY. Whitstable, Kent, England, on shell of *Ostrea edulis* Linnaeus, 1758 (Ellis, 1755 : pl. 10, figs A, a, B) ; location of specimens unknown.⁸

MATERIAL EXAMINED. Oban, Argyll, 1877, three colonies in spirit, coll. A. M. Norman, 1912.12.21.198. Bridlington Bay, Yorkshire, 7 Nov. 1921, several colonies in spirit, coll. S.S. 'George Bligh', 1956.2.2.26. S edge of Smith's Knoll, off Norfolk, 19 Jan. 1905, part of ♀ colony on microslide, coll. M.V. 'Goldseeker', det. J. Ritchie, 1964.8.7.273 (mentioned, Rees & Thursfield, 1965 : 105). Isle of Man, 5 Jul. 1894, part of ♀ colony on microslide, coll. E. T. Browne, 1959.9.17.5 (Fig. 6). Menai Straits, Anglesey, Jul. 1964, part of ♂ colony on microslide, coll. W. J. Rees, 1969.12.1.2. R. Deben estuary, Suffolk, several ♂ colonies in spirit, coll. D. L. Serventy, 1933.7.1.12. East Solent, Hampshire, part of infertile colony on microslide, coll. A. Dendy, 1886.10.4.6. Off Lulworth, Dorset, 7 m, fragments of

⁸ Linnaeus quoted the earlier designations of Ray (1724) and Ellis (1755) and probably saw no material himself since he did not give a locality. Although the collections of the Linnean Society of London include material labelled *H. halecinum* [catalogued 1298.7-8 by Savage (1945)], it was probably added to the collection after 1758. Furthermore, none of it is the species currently recognized under this name. The specimens comprise two fertile colonies of *H. beanii* (sheet 7) and a colony of *Sertularella* sp. (sheet 8).

Although some of Ray's and Ellis' material was later incorporated in the Hans Sloane herbarium, now in the British Museum (Natural History), there is no indication that the specimens of *H. halecinum* [H.S. 150 : 37 (R.H. 79) ; H.S. 114 : 1 (12)] in the Sloane herbarium are theirs since they have no collector's name or locality. They cannot, therefore, be identified as type material.

Some Ellis hydroid material, which might have included the originally illustrated specimens of *H. halecinum*, was until recently preserved in the Hunterian Museum of the Royal College of Surgeons of England. Unfortunately, the Ellis material was almost certainly destroyed by a bomb during the Second World War and no *Halecium* material survives (see Cornelius, 1975 : 267, footnote, for details).

♂ colony on two microslides, coll. F. Beckford, 1889.7.27.7. Tor Bay, Devon, 1875, part of ♂ colony on microslide, coll. A. M. Norman, 1898.5.7.86 (Fig. 6). Start Point, Devon, 18 m, part of ♀ colony on microslide, coll. R. Kirkpatrick, 1893.8.7.4. Plymouth, Devon, 19 Dec. 1892, part of ♂ colony on microslide, coll. E. T. Browne, 1959.9.17.4. Manacle Rocks, Porthoustock, Lizard Peninsula, Cornwall, 18 m, 29 Aug. 1965, part of ♂ colony on microslide, coll. R. Davis, pres. R. C. Vernon, 1966.1.1.3.

DESCRIPTION. Colony stiffly erect, regularly pinnate, with second and some third order branching. Hydrocaulus and main branches polysiphonic basally, component perisarc tubes branching off successively in groups; final branches monosiphonic, straight or slightly flexuose. Internodes equal, with distal hydrophore. Hydrothecae alternate, short, rim even, slightly flared, secondary, tertiary and some quaternary hydrothecae inside primary (Fig. 6) and longer than it. Hydranth larger than hydrotheca, hypostome conical, 17–22 tentacles. ♂ gonotheca club-shaped, tapering basally, rounded distally; ♀ gonotheca oblong, tapering basally, subtruncate distally with lateral tubular aperture, 1–4 ova, with 1–3 hydranths projecting through aperture. Sexes on separate colonies.

MEASUREMENTS. See Table 5.

TABLE 5

Halecium halecinum. Measurements in μm unless otherwise stated

	? U.S.S.R. (Naumov, 1969)	NETHERLANDS (Vervoort, 1946)	SE ENGLAND (1964.8.7.273)	SW ENGLAND (1889.7.27.7)
HYDROTHECA				
Length (diaphragm to rim)	90–150	—	20–40	25–40
Breadth at rim	170–210	100–200	140–165	130–145
Hydrocaulus diameter (min.)	—	—	190–225	100–150
Length of internodes	—	—	350–380	280–400
♂ GONOTHECA				
Length	—	800–1000	—	700–800
Breadth (max.)	—	c. 400	—	250–400
♀ GONOTHECA				
Length	2000	1000–1300	1250–1400	—
Breadth (max.)	500	400–500	350–600	—
MAXIMUM HEIGHT OF COLONY	0.25 m	0.25 m	—	—

REPRODUCTIVE SEASON. Fertile specimens recorded December to July in English Channel and off Norfolk (Hamond, 1957; Marine Biological Association, 1957; Teissier, 1965); one fertile ♂ specimen 29 August, S Cornwall (1966.1.1.3).

DISTRIBUTION. Common throughout British Isles and adjacent continental shelf areas.

HABITAT. On stones, shells and other hard substrates, from sublittoral to edge of continental shelf and sometimes deeper (Broch, 1918). Detached fragments frequently occur on strand-line.

REMARKS. *Halecium geniculatum* Norman, 1867, appears from the original description to be conspecific with *H. halecinum*. The long, tubular hydrothecae described by Norman and regarded by him as diagnostic were probably just the renovated hydrophores which normally occur in *H. halecinum*.

***Halecium labrosum* Alder, 1859**

(Fig. 7)

? *Eudendrium pusillum* Sars, 1857: 154, pl. 1, figs 14-16.

Halecium labrosum Alder, 1859: 354, pl. 13; Hincks, 1868: 225-226, pl. 44, fig. 1, text-fig. 27; Rees & Thursfield, 1965: 107-108 (syn. *H. crenatum* Hincks, 1874a); Naumov, 1969: 489-490, fig. 343; Calder, 1970: 1506-1508, pl. 1, figs 6-8.

Halecium pusillum: Kossowska, 1911: 347-350, figs 15-16; Broch, 1912: 16-17, fig. 2; Bedot, 1916: 115-116; [? non Teissier, 1965: 21; see Remarks].

Halecium annulatum Stechow, 1919: 33 (nom. nov. pro *H. pusillum*: Kossowska).

Halecium reflexum Stechow, 1919: 37-39, figs G-H; Teissier, 1965: 21.

Halecium undulatum Billard, 1921: 137-139, fig. 3; Leloup, 1952: 144-145, fig. 79; Hamond, 1957: 304-307, figs 12, 13 [syn. *H. tenellum*: Broch, 1918 (part); Kramp, 1929 (part); Kramp, 1932 (part); Kramp, 1938 (part)]; Hamond, 1963: 667; Calder, 1970: 1510-1512, pl. 2, figs 7-9; (syn. nov.).

Halecium tenellum: Fraser, 1944: 201-203, pl. 37, fig. 179 (part); Leloup, 1952: 144, fig. 77 (part).

Halecium schneideri: Leloup, 1952: 144, fig. 78 (? non *H. schneideri* Bonnevie, 1898).

TYPE MATERIAL AND LOCALITIES. Syntypes: Large infertile colony on herbarium sheet and a fertile spirit specimen, probably male, in four pieces, both labelled 'deep water, Northumberland coast', Hancock Museum, Newcastle-upon-Tyne. Other type localities: Moray Firth and Shetland (Alder, 1859).

MATERIAL EXAMINED. Vattestraumen channel, Hardanger Fjord, Norway, 60°20' N, 5°12' E, 15-25 m, 13 Apr. 1962, several colonies in spirit, three microslides of fragments (2 ♂, 1 sterile), coll. W. J. Rees, 1962.10.7.13 (Fig. 7), 35, 66. N Väderö Is., Skagerrak, 58°35' N, 11°04' E, 80 m, 1 Oct. 1964, colony in spirit and one microslide, coll. W. J. Rees, 1965.1.14.135 (Fig. 7). Firth of Lorn, Argyll, Scotland, 120-140 m, part of colony on microslide, coll. J. Murray, 1888.6.9.6. Mull of Kintyre, Argyll, Scotland, 90 m, two ♀ colonies in spirit and two microslides, coll. J. Murray, 1888.1.24.19 (Fig. 7). Plymouth, Devon, England, 17 Aug. 1898, six fragments of ♀ colonies on microslide, coll. E. T. Browne, 1959.9.17.9. Eddystone ground, western English Channel, 15 Sep. 1897, several fragments of colonies in spirit, coll. E. T. Browne, 1941.3.20.413. Eddystone ground, western English Channel, 19 Nov. 1897, parts of colonies on two microslides, coll. E. T. Browne, 1959.9.17.6, 123. Messina, Sicily, Italy, infertile colony on alga in spirit, holotype of *Halecium pusillum* Sars, 1857, Oslo Zoological Museum Cat. No. B1156 (mentioned, Broch, 1912; see Remarks, below).

DESCRIPTION. Colony erect, up to c. 50 mm, imperfectly pinnate, all but final branches polysiphonic; main branches slightly flexuose, side-branches inserted alternately with characteristic curve near base. Living tissues said to be purplish (Hincks, 1868). Internodes unequal, perisarc transversely wrinkled over much or

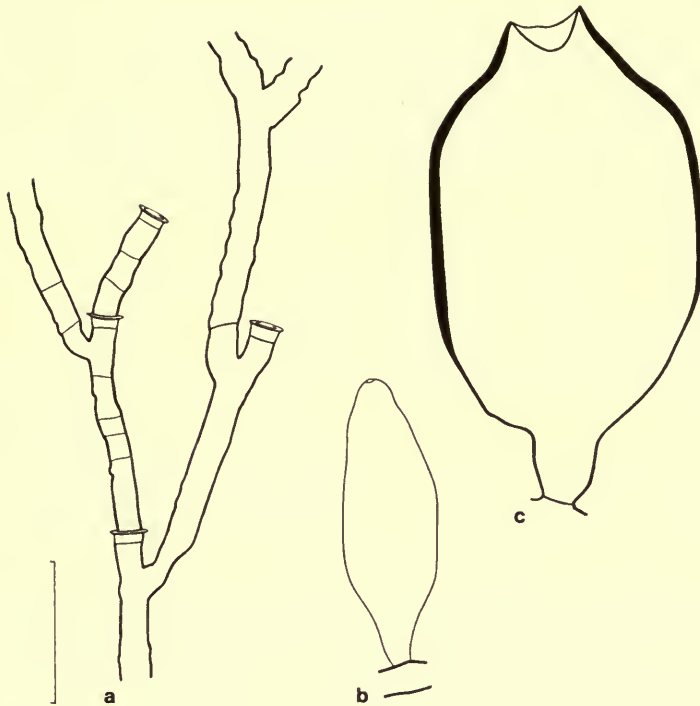


FIG. 7. *Halecium labrosum*. a, part of colony, Skagerrak, 80 m (1965.1.14.135); b, ♂ gonotheca, near Bergen, Norway, 15–25 m (1962.10.7.13); c, ♀ gonotheca, W Scotland, 90 m (1888.1.24.19). Scale (a–c) = 500 μ m.

all of length or, occasionally, smooth. Hydrothecae sessile, borne on prominent hydrophores, short, rims strongly recurved; up to c. 12 renovations common. Gonothecae on 1- or 2-ringed pedicel; gonothecal hydranths absent; ♂ ovate to linear, tapering basally and sometimes distally also, aperture simple, terminal; ♀ ovate, larger than ♂, aperture simple, terminal; sexes on separate colonies.

MEASUREMENTS. See Table 6.

REPRODUCTIVE SEASON. Incompletely known. Fertile specimens recorded early May in southern North Sea, late May in Orkneys and Faroes, late June in Iceland (Hamond, 1957); 17 August 1898 at Plymouth (present material); September at Roscoff (Teissier, 1965).

DISTRIBUTION. A northern species known from localities throughout British coastal waters (Hincks, 1868; Hamond, 1957; Marine Biological Association, 1957). Although recorded from Roscoff, NW France (Teissier, 1965), the species appears absent from the Scilly Isles, Channel Islands, Belgium and Holland (Vervoort, 1946, 1949; Leloup, 1952; Robins, 1969) and the English Channel is probably near its southern limit. The species is known from the Danish coast and the Skagerrak (Kramp, 1935) but has been reported absent from the Baltic (Broch, 1928).

TABLE 6

Halecium labrosum. Measurements in μm

	W ENGLISH CHANNEL (1959.9.17.123)	PLYMOUTH (1959.9.17.9)	ARGYLL, SCOTLAND (1888.1.24.19)	W NORWAY (1962.10.7.13)
HYDROTHECA				
Length (diaphragm to rim)	30-50	30-45	40-50	30-45 (one 60)
Breadth at rim	240-280	150-165	220-255	140-155 (one 170)
Hydrocaulus diameter (min.)	160-200	90-110	130-150	90-110
Length of internodes	950-1175	800-1700	550-700	600-820
♂ GONOTHECA				
Length	—	—	—	700-1000
Breadth (max.)	—	—	—	300-900
♀ GONOTHECA				
Length	—	640-1100	1350-1580	—
Breadth (max.)	—	470-530	950-1090	—

HABITAT. Offshore, 5-200 m; found epizoic on exoskeletons of various invertebrates (Hamond, 1957) and probably occurs also on inanimate substrates.

REMARKS. The variation in transverse wrinkling of the internodal perisarc in this species has caused systematic confusion. As noted by Hamond (1957), specimens with completely smooth internodes have probably been confused with *H. tenellum* Hincks, 1861, which is, however, smaller in all dimensions, seldom has a wrinkled perisarc and lacks the curvature of the bases of the hydrocladia typical of *H. labrosum*.

Eudendrium pusillum Sars, 1857, type locality northern Sicily, remains problematical. It was recognized as *Halecium* by Kossowska (1911) who wrongly included *H. lankesteri* in its synonymy. Broch (1912) redescribed and figured part of the holotype and regarded the species as valid. The type material, re-examined here, has a recurved hydrothecal rim, a feature noted by Broch but not by Sars, and this and the curving bases of the branches are reminiscent of the present species. However, identification is made difficult by the type material being sterile and stunted in comparison with colonies of *H. labrosum*. It is not, therefore, possible to identify it confidently with the present species, which in addition has not been recorded so far south. Possibly the material from NW France identified as *H. pusillum* by Teissier (1965) was in fact *H. labrosum* as defined here; his is apparently the only suggestion that *H. pusillum* occurs in the present area.

Halecium reflexum Stechow, 1919, appears from the original description to resemble *H. labrosum* in its manner of branching, recurved hydrothecal rim and wrinkled perisarc, and the two taxa appear conspecific.

Halecium undulatum Billard, 1921, seems to have been based merely on small colonies of *H. labrosum*. The two taxa appear similar in all characters except colony size and their distributions coincide so that there seems no reason to keep them distinct. Consequently the many *H. tenellum* records referred to *H. undulatum*

by Hamond (1957) are identified here as *H. labrosum*. The gonothecae described by Calder (1970) under *H. undulatum* are similar to those of *H. labrosum* s. str.

The material described by Leloup (1947, 1952) under the name *H. schneideri* Bonnevie, 1898, is here referred to the present species. *H. schneideri* was a new name for *H. nanum* Alder, 1859, a species otherwise unrecorded from the present area. It was redescribed by Fraser (1944).

***Halecium lankesteri* (Bourne, 1890)**

(Fig. 8)

Halecium robustum Pieper, 1884 : 166–167 ; Babič, 1913 : 470–473, figs 1–7 ; Bedot, 1914 : 82 ; Stechow, 1919 : 39–40 ; Teissier, 1965 : 21 ; Fey, 1969 : 397 ; [non *Halecium robustum* Verrill, 1873 : 9 ; (= *Zygophylax* sp. ; see p. 402)].

Haloikema lankesterii Bourne, 1890 : 395–396, pl. 26.

Halecium lankesteri : Bedot, 1911 : 213–217, pl. 11, figs 1–5 (= *H. sessile* : Billard, 1904) ; Stechow, 1923 : 88 ; Prenant & Teissier, 1924 : 25 ; Broch, 1933 : 16–17, fig. 3 ; Vervoort, 1949 : 145 ; Hamond, 1957 : 302–304, figs 9–10 ; Marine Biological Association, 1957 : 46 ; Vervoort, 1959 : 221–224, figs 3–5 ; Millard, 1968 : 257–258, fig. 1.

NOMENCLATURE. The species was named after Professor E. R. Lankester.

TYPE MATERIAL AND LOCALITY. Syntypes : Near Duke Rock Buoy, Plymouth Sound, Devon, England, May 1889, several infertile colonies in spirit, coll. G. C. Bourne, 1974.2.28.1. Remaining type material recorded from Jennycliff Bay, Plymouth Sound, May 1890, not located.

OTHER MATERIAL EXAMINED (All BM(NH) material except types). Studland Bay, Dorset, England, 6–8 m, ♀ colonies on six microslides, coll. R. Kirkpatrick, pres. F. Beckford via A. M. Norman, 1890.7.22.5 (Fig. 8). Mewstone, off Wembury, Devon, infertile colony on *H. halecinum*, in spirit, coll. E. T. Browne, 1948.10.1.125 (Fig. 8). Plymouth, Devon, 15 Jul. 1898, infertile fragments on microslide, coll. E. T. Browne, 1959.9.17.1. Plymouth, Devon, 1892, several infertile colonies in spirit, coll. W. Garstang, pres. A. M. Norman, 1912.12.21.572. E of Duke Rock Buoy, Plymouth, on piece of wire, c. 10 m, 2 Jul. 1973, dense growth of ♂ colony in spirit and hydrocaulus on microslide, coll. P. F. S. Cornelius, 1974.3.1.1 (Fig. 8 ; duplicate spirit material deposited in the Museum of the Marine Biological Association, Plymouth).

DESCRIPTION. Colony erect, up to c. 80 mm, usually unbranched but sometimes imperfectly pinnate ; monosiphonic. Internodes often irregular in length, 0–10 (usually 1) annulations between hydrothecae ; bases of hydrocladia often curved inwards sharply. Hydrotheca on prominent hydrophore at distal end of internode ; usually alternate ; slightly tapering basally, short ; rim not flared ; up to c. 5 hydrothecal renovations. Hydranth large, 10–20 tentacles. Gonotheca on short pedicel below a hydrotheca. ♂ cylindrical, aperture terminal ; ♀ kidney-shaped with tubular aperture in centre of concave side, 3–20 ova, 1–2 protruding polyps. Vervoort (1959) records sexes on separate colonies, ♂ gonothecae ‘exclusively on renovated hydrophores’ over entire colonies, ♀ on lower parts of colonies on secondary or tertiary hydrophores.

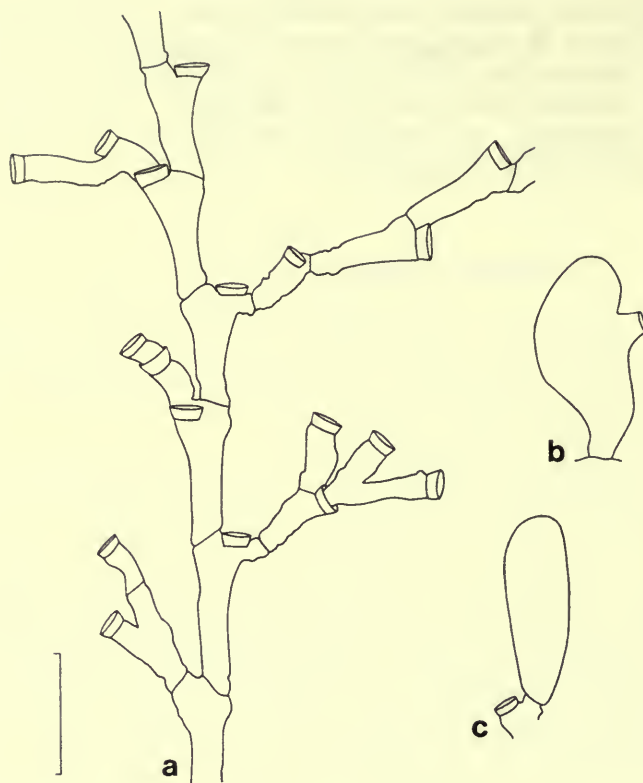


FIG. 8. *Halecium lankesteri*. a, part of colony, SW England (1948.10.1.125); b, ♀ gonotheca, SW England, 6–8 m (1890.7.22.5); c, ♂ gonotheca, SW England, c. 10 m (1974.3.1.1). Scale (a–c) = 500 μ m.

MEASUREMENTS. See Table 7.

VARIATION. Hydrocladia may or may not appear to be sharply incurved basally, and Fig. 8 shows a specimen with both conditions. There may be 0–10 internodal annulations between hydrothecae, and successive internodes are not identical in shape or length. The degree of wrinkling of the perisarc is variable. Tendril development occurs (e.g. 1974.3.1.1) but is unusual.

REPRODUCTIVE SEASON. June–July at Roscoff (Teissier, 1965); gonothecae of both sexes, Norfolk coast, 26 June 1952 (Hamond, 1957); ♂ gonothecae, Plymouth, Devon, 2 July 1973 (1974.3.1.1). Infertile material from Plymouth includes the type specimens collected May 1889 and May 1890, and other material collected 15 July 1898 (1959.9.17.1).

DISTRIBUTION. There are published records from NW France, the Channel Islands, SW England, SW Wales and Norfolk (Bourne, 1890; Vervoort, 1949;

TABLE 7

Halecium lankesteri. Measurements in μm unless otherwise stated

	SW ENGLAND (1974.2.28.1 ; type)	SW ENGLAND (1974.3.1.1)	GUINEA (Vervoort, 1959)	MOZAMBIQUE (Millard, 1968)
HYDROTHECA				
Length (diaphragm to rim)	45-70	30-35	20-25	30-40
Breadth at rim	200-230	130-140	120-130	140-150
INTERNODES				
Diameter (min.)	150	90-110	—	—
Length	550-750	320-600	420-540	200-660
♂ GONOTHECA				
Length	—	610-720	410-510	—
Breadth (max.)	—	200	200-240	—
♀ GONOTHECA				
Length	—	—	880	520-650
Breadth (max.)	—	—	450	380-450
MAXIMUM HEIGHT OF COLONY	c. 3 mm	c. 40 mm	c. 8 mm	c. 5 mm

Hamond, 1957 ; Teissier, 1965 ; Fey, 1969). The present records fall within this distribution and southern British waters appear to be the northern limit of this species. It does not appear to have been recorded from Ireland. The distribution abroad was summarized by Stechow (1923), Broch (1933), Vervoort (1959) and Millard (1968).

HABITAT. Recorded on stones (Bourne, 1890), other hydroids, crabs and Bryozoa (Hamond, 1957 ; Vervoort, 1959 ; present material), and on algae (Teissier, 1965 ; Fey, 1969). 0-c. 50 m depth ; not recorded intertidally.

REMARKS. The most useful descriptions of this species are those of Bourne (1890), Bedot (1911), Broch (1933), Vervoort (1949, 1959), Hamond (1957) and Millard (1968).

The measurements of the type material given here appear high in comparison with those of the other measured material. There is, however, no doubt that the type material is referable to the concept of the species both as first described by Bourne (1890) and as understood by recent authors (Hamond, 1957 ; Vervoort, 1959 ; Millard, 1968). The type specimens lack a flared hydrothecal rim which might otherwise identify them as *H. labrosum* Alder, 1959. They resemble closely the illustrations of Bedot (1911).

Although the hydranths of the type specimens were brown (Bourne, 1890), colourless and green hydranths have been recorded (Vervoort, 1949) and hydranth colour cannot be regarded as a useful specific character.

The confusion between *Halecium lankesteri* and the several species to which the combination *Halecium robustum* has been applied was summarized by Hamond (1957). The earliest usage, *H. robustum* Verrill, 1873, referred to a species of

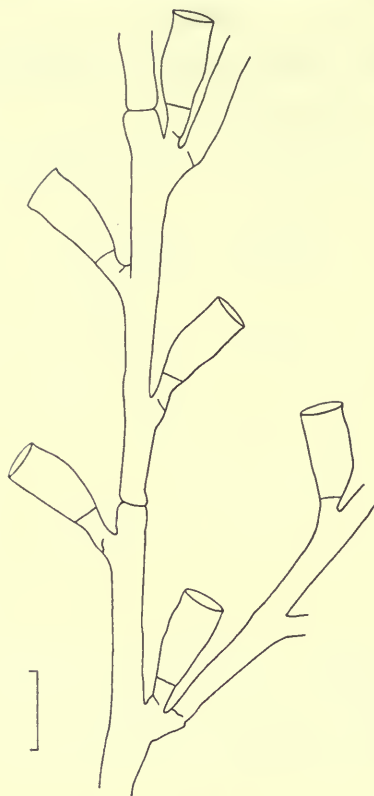


FIG. 9. Part of neotype of *Halecium robustum* Verrill, 1873, Massachusetts (Yale Peabody Museum No. 9137). Scale = 500 μ m. The specimen is here referred to the genus *Zygophylax*.⁹

Zygophylax so that the name *robustum* is not available for a *Halecium* species.⁹ *H. lankesteri* (Bourne, 1890) is the next available name for the present species.

***Halecium muricatum* (Ellis & Solander, 1786)**

(Fig. 10)

Sertularia echinata Linnaeus, 1761 : 541 (part) ; Pallas, 1766 : 152 (part) ; Linnaeus, 1767 : 1310 (part).

Sertularia muricata Ellis & Solander, 1786 : 59-60, pl. 7, figs 3-4.

⁹ The holotype of the nominal species *Halecium robustum* Verrill (1873 : 9; 786 m, St George's Bank, E Canada, 15 Sep. 1872, Yale Peabody Museum No. 3651) was never illustrated and is now lost (W. D. Hartman, pers. comm.) but a non-type specimen, labelled *H. robustum* in Verrill's hand, is extant and is here made neotype of *H. robustum* (off Cape Ann, Massachusetts, 17 Sep. 1878, branched hydrocaulus on microslide, YPM No. 9137). The specimen (Fig. 9) has the characters of *Zygophylax* sensu Totton (1930). Thus the specific name *robustum* is not available for a *Halecium* species; and the species described by Verrill should be known as *Zygophylax robustum*. It predates other species of *Zygophylax*, but as specific limits within that genus are at present unclear no new synonymy is proposed. However, it may be noted that in lacking nematothecae and in having campanulate, straight or only slightly curved hydrothecae the neotype specimen resembles closely the original illustrations of *Z. pinnata* (Sars, 1874).

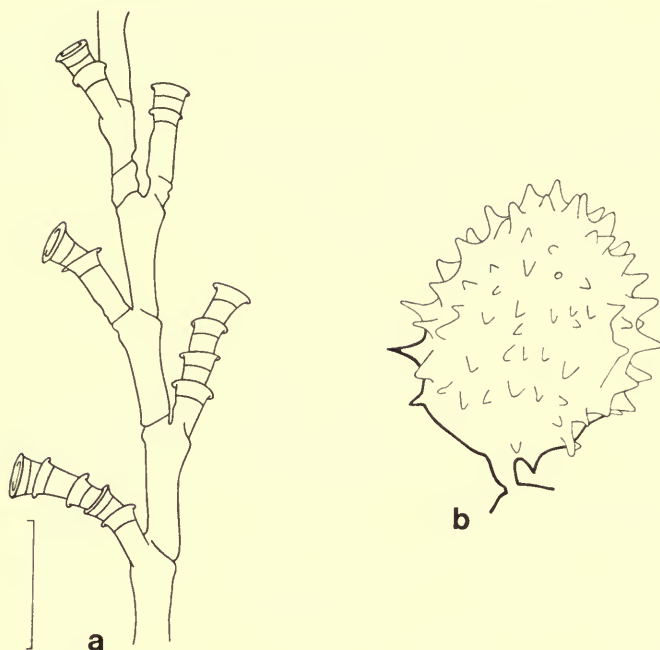


FIG. 10. *Halecium muricatum*. a, part of colony, E Scotland, 55 m (1969.12.5.9); b, ♀ gonotheca (identified from contents; ♂ is externally similar), E Scotland, 20 m (1964.8.7.87). Scale (a-b) = 500 µm.

Halecium filiforme Alder, 1862a : 315 (part); Alder, 1862b : 236 (part); Hincks, 1868 : 228 (part).

Halecium muricatum : Hincks, 1868 : 223–224, pl. 43, figs 1, 1a–b; Broch, 1918 : 43–45, fig. 17; Fraser, 1944 : 197–198, pl. 37, fig. 176; Vervoort, 1946 : 163–164, fig. 67; Naumov, 1960 : 456–457, fig. 347; Naumov, 1969 : 492–493, fig. 347; Vervoort, 1972 : 27, fig. 3b–d.

Halecium murigatum Williams, 1954 : 48 (lapsus pro *muricatum*).

TYPE LOCALITY AND MATERIAL. The original description was based on material supplied by a Dr David Skene of Aberdeen, but no locality was given and the specimen has not been located (see also footnote 8, p. 394). The type locality is here restricted to near Aberdeen, Scotland.

MATERIAL EXAMINED. Firth of Lorn, Argyll, Scotland, 130–150 m, part of infertile colony on microslide, coll. J. Ritchie, 1974.3.7.1. Off SE coast of Isle of Mull, Argyll, 10 Apr. 1971, two colonies in spirit, coll. P. F. S. Cornelius, 1971.5.11.30. Moray Firth, E Scotland, 55 m, 8 Dec. 1965, fertile fragments on two microslides, coll. F. W. E. Rowe, 1969.12.5.9 (Fig. 10). Burghead Bay, Moray Firth, 20 m, 22 Nov. 1905, fertile fragments on microslide, coll. J. Ritchie, 1964.8.7.87 (Fig. 10; mentioned, Rees & Thursfield, 1965 : 109). Gullmarfjord, Sweden, 20–30 m, 27 Aug. 1962, fragment on microslide, coll. W. J. Rees, 1962.11.8.15. Probably W coast of Sweden, about 1758–60, 30 mm portion of fertile colony, Linnaeus colln., Linnean Society of London Catalogue No. 1298.14 (not type material; see Remarks).

DESCRIPTION. Colony erect, up to 100 mm, rarely 200 mm, imperfectly pinnate ; main stem and larger branches polysiphonic ; hydrocladia alternate. Nodes equally spaced, annulations often sloping alternately left and right but sometimes transverse. Hydrothecae alternate, on the monosiphonic branches, distal hydrophore usually demarcated by deep, irregular annulus ; hydrotheca short, rim even, usually flared but sometimes straight ; commonly up to *c.* 6 renovations. Gonothecae ovoid, pedicellate, with numerous 100–200 μ m spines, in 9–15 rows. Sexes generally reported similar (see Remarks).

MEASUREMENTS. See Table 8.

TABLE 8

Halecium muricatum. Measurements in μ m

	SE SCOTLAND (1964.8.7.87 ; Fig. 10)	SW SCOTLAND (1974.3.7.1)	W SWEDEN (1962.11.8.15)
HYDROTHECA			
Length (diaphragm to rim)	30–80	35–50	40–60
Breadth at rim	130–160	140–170	240–280
INTERNODE			
Length	480–600	600–800	850–1100
Minimum breadth	80–110	100–180	130–150
GONOTHECA ($\delta = \varnothing$)			
Length	1000–1500	—	—
Breadth	900–1300	—	—

REPRODUCTIVE SEASON. Little information. Fertile material recorded from Norfolk, 16 Nov. 1960 (Hamond, 1963) and in the British Museum (Natural History) collections from the Moray Firth, Scotland, 22 Nov. 1905 (1964.8.7.87) and 8 Dec. 1965 (1969.12.5.9). The apparent autumn breeding of this species in British waters is perhaps related to its northerly distribution. In Oslofjord specimens with gonothecae have been recorded in December and February and also in June (Christiansen, 1972) but it is not clear if the June material was living when collected.

DISTRIBUTION. An arctic and northern boreal species, extending south to the coasts of Scotland, NE England, Denmark and Sweden with occasional records in the central North Sea, Dogger Bank and off the Norfolk coast (Hincks, 1868 ; Broch, 1928 ; Kramp, 1935 ; Hamond, 1957, 1963 ; Rees & Rowe, 1969 ; Christiansen, 1972). Other records include SW Scotland (Vervoort, 1946 ; present material), Isle of Man (Bruce *et al.*, 1966), Co. Antrim and Co. Down, Northern Ireland (Hincks, 1868 ; Stephens, 1905 ; Williams, 1954, in 1857). The species has not been included in recent faunal surveys of the following areas : Roscoff (Teissier, 1965), Scilly Isles (Robins, 1969), Plymouth (Marine Biological Association, 1957), Pembrokeshire (Crothers, 1966) and Anglesey (K. Hiscock, pers. comm.) ; and further eastwards was not reported from Belgium (Leloup, 1952), Holland (Vervoort, 1946) and the coast of Germany (Broch, 1927). There is apparently no record from the English Channel since Hincks (1868) recorded the species from Cornwall and South Devon, and no record this century from Irish waters.

HABITAT. Mainly 10–200 m in Russian seas (Naumov, 1969), occurring down to 1350 m in the North Atlantic (Broch, 1918); not intertidal. Recorded on both hard substrates such as shells and rocks (Hincks, 1868) and on red algae (Christiansen, 1972).

REMARKS. The combination *Sertularia echinata* Linnaeus, 1761, was used in several works between 1761 and 1802 (Bedot, 1901), but the specific name was apparently not used between then and 1910 (Bedot, 1905, 1910, 1912, 1916, 1918, 1925) and has apparently not been used since. The taxon was tentatively referred to the present species by Johnston (1838: 121; 1847: 61) and later by Vervoort (1946: 163) but it appears that this action was only partly correct. The type material of *S. echinata* is preserved in the collections of the Linnean Society of London, on herbarium sheet No. 1298.14 (Savage, 1945). The sheet bears two specimens. That on the left comprises two infertile colonies arising from a common substrate, each referable to *Sertularia cupressina* Linnaeus, 1758. That on the right, however, is a fertile fragment 30 mm long referable to *H. muricatum* as defined above. The original diagnosis of *S. echinata* was probably made from both the specimens, as it includes characters of both *S. cupressina* ('denticulis oppositis obtusiusculis') and of *H. muricatum* ('calycibus [gonotheca] obovatis compressis reticulatis muricatis'). The specimen on the left of the sheet is here nominated as lectotype, so that the name *S. echinata* Linnaeus, 1761, falls into the synonymy of *S. cupressina* Linnaeus, 1758. The later descriptions of *S. echinata* provided by Pallas (1766) and Linnaeus (1767) perpetuated Linnaeus' (1761) confusion of the two species. The first available name for the present species is thus *Sertularia muricata* Ellis & Solander, 1786.

Halecium filiforme Alder, 1862a, was described only briefly by Alder without illustration (1862a, b) and the description was repeated by Hincks (1868). Hincks considered the species closest to '*H. plumosum*' (= *H. sessile*; see p. 409) but quoted Alder as later regarding *H. filiforme* as 'probably a mere variety or an immature state of some other species'. The original description agrees with '*H. plumosum*' in the following characters: hydrocaulus 'very slender, flexible', monosiphonic, little branched; length 115 mm ($4\frac{1}{2}$ inches); 'branchlets' arising from the side of a hydrotheca; and differs in that the hydrothecae are said to be 'rather slender, tubular, with a slightly everted margin'. The type material of *H. filiforme* in the Hancock Museum, Newcastle-upon-Tyne, is a mixed series comprising specimens referable to both *H. muricatum* and *H. sessile* Norman, 1867. The herbarium specimen labelled '*Halecium filiforme*, deep water, Northumberland' is here designated lectotype of *H. filiforme*. It is a large infertile colony of *H. muricatum*, of which name *H. filiforme* thus becomes a junior synonym. The Newcastle-upon-Tyne material will be more fully described elsewhere (Cornelius & Garfath, in prep.).

Most authorities have considered the gonothecae of the two sexes identical (e.g. Hincks, 1868; Fraser, 1944; Vervoort, 1946), but Rees & Thursfield (1965: 109) implied that there is a difference without providing details of how they differ. The weight of opinion at present suggests that there is no difference, however.

Halecium sessile Norman, 1867

(Fig. 11)

- Halecium filiforme* Alder, 1862a : 315 (part) ; Alder, 1862b : 236 (part) ; Hincks, 1868 : 228 (part) ; (see p. 405).
Halecium sessile Norman, 1867 : 205 ; Hincks, 1868 : 229-230, pl. 44, fig. 2 ; Storm, 1882 : 19 (? syn. *H. plumosum*) ; Billard, 1904 : 52-53, 157-160 ; pl. 3, figs 8-9, pl. 6, figs 1-14 ; Kuhn, 1913 : 139, fig. 58 ; Vervoort, 1941 : 195-196 ; Ralph, 1958 : 331-332, figs 9h-i, 10c-d ; Teissier, 1965 : 21 ; Vervoort, 1966 : 100-102, fig. 1 (syn. *H. kofoidi* Torrey, 1902 ; *H. lighti* : Nutting, 1927) ; Christiansen, 1972 : 298.
Halecium plumosum Hincks, 1868 : 227-228, pl. 64, fig. 1 ; Kuhn, 1913 : 70, 112, fig. 46 ; Christiansen, 1972 : 299 ; (syn. nov.).
Halecium articulatum Clarke, 1875 : 63, pl. 10, fig. 6 ; Jaderholm, 1909 : 58, pl. 5, fig. 7 ; Kramp, 1935 : 149-150, fig. 62c ; Kramp, 1938 : 32 ; Fraser, 1944 : 185-186, pl. 33, fig. 159 ; Leloup, 1952 : 143-144, fig. 76 ; Christiansen, 1972 : 299 ; (syn. nov.).

TYPE MATERIAL AND LOCALITY. 'Deep water in the Minch', between Outer Hebrides and mainland Scotland ; specimen not located.

MATERIAL EXAMINED.¹⁰ Gullmarfjord, W Sweden, c. 30 m, 13 Jan. 1910, colony in spirit, coll. T. Mortensen, Copenhagen Zoological Museum (CZM). Gullmarfjord, W Sweden, 15 Oct. 1918, colony in spirit with epizoic *Halecium beanii*, coll. Kristineberg Zoological Station, CZM. 22 km N of Hirtshals, Denmark, 110 m ('Thor' sta. 1576), 27 Jun. 1911, colony in spirit, CZM. Nr Fredrikshavn, Denmark, 17 m, 13 Aug. 1930, coll. P. L. Kramp, CZM. Oresund, Denmark, c. 25 m, 27 Aug. 1928, CZM.

Great Cumbrae Island, R. Clyde, W Scotland, 15-30 m, 18 May 1955, colony in spirit plus one microslide, coll. W. J. Rees, 1956.1.1.16. Salcombe, Devon, on *Nemertesia* sp., infertile colony in spirit, coll. T. Hincks, 1899.5.1.167. Near Eddystone Rock, off SW coast of England, 10 Sep. 1897, infertile colony in spirit and fragments on microslide, coll. E. T. Browne, 1941.3.20.414. 3 km E of Eddystone Rock, 6 Jul. 1971, two infertile colonies in spirit plus one microslide, coll. P. F. S. Cornelius, 1971.7.10.1. 4 km NNW of Eddystone Rock, c. 40 m, 20 Jul. 1972, infertile colony in spirit, coll. P. F. S. Cornelius, 1973.11.22.7. Bay of Biscay, 7 Mar. 1912, fragments of ♂ colony on microslide, coll. E. T. Browne, 1959.9.17.8. Off R. Sado, Portugal, infertile colony in spirit, coll. W. Saville Kent, 1872.2.3.137. South of Terceira Island, Azores, 610 m, Aug. 1959, infertile colony and fragments on microslide, coll. Imperial College (University of London) Azores Expedition, 1962.1.15.12.¹¹ Bay of Fundy, New Brunswick, Canada, 1872, 30 mm infertile colony in two parts, coll. U.S. Fisheries Commission (U.S.F.C.), Yale Peabody Museum (YPM) 3478. Casco Bay, Maine, U.S.A. 1873, five fragments of colonies (four infertile, one ♀), coll. U.S.F.C., YPM 5460 (syntypes of *Halecium articulatum* Clarke, 1875). Eastport, Maine, U.S.A. 1868, eight fragments of colonies (five infertile, three ♀), coll. A. E. Verrill, YPM 3663-4. Eastport, Maine, U.S.A. 1868, 40 mm colony, coll. A. E. Verrill & S. I. Smith, YPM 3477. Jarvis Bay, New South Wales, Australia, c. 20 m, 1898, infertile fragment on microslide, coll.

¹⁰ The Danish and Swedish material is that mentioned by Kramp (1935 : 150) as *Halecium articulatum*.

¹¹ The microslide specimen has an epizoic colony of *Lafoeina* sp., a genus not previously recorded from the Azores (Rees & White, 1966).

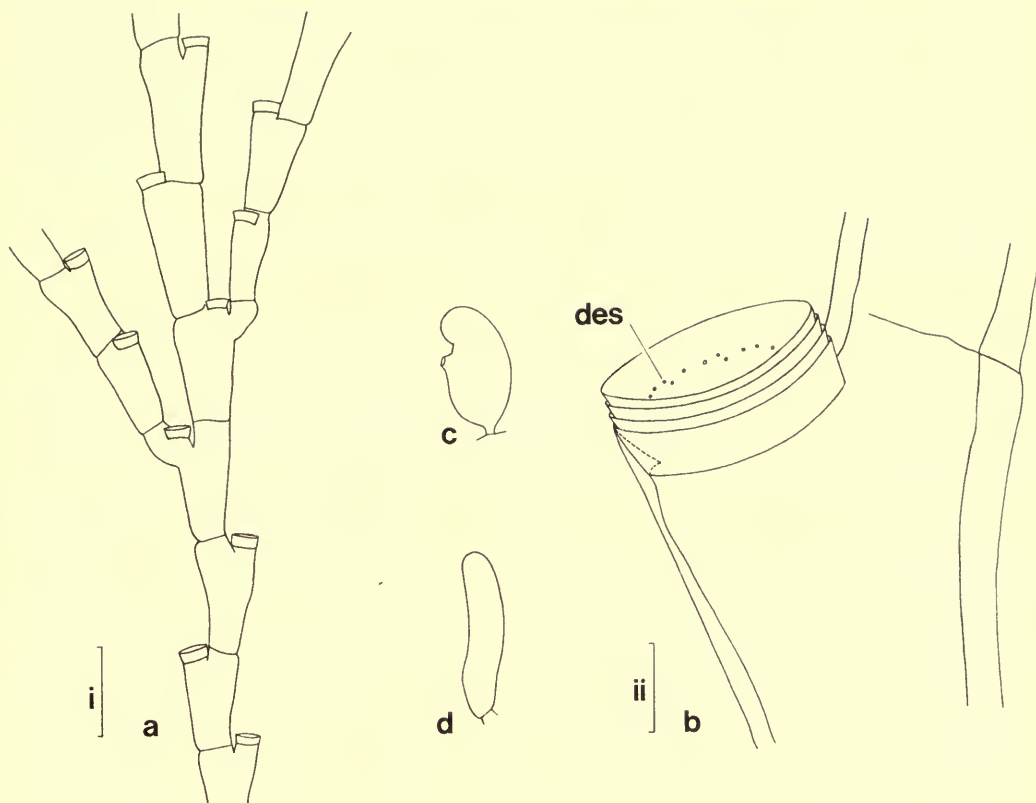


FIG. 11. *Halecium sessile*. a-b, part of colony and one hydrotheca, SW England (1971.7.10.1); c, ♀ gonotheca, N France (redrawn after Billard, 1904: pl. 6, fig. 14); d, ♂ gonotheca, Bay of Biscay (1959.9.17.8). Scale i (a, c, d) = 500 μ m; scale ii (b) = 50 μ m. des. = desmocyte ('puncta').

H.M.S. 'Thetis', ex J. Ritchie collection, 1964.8.7.88 (mentioned, Rees & Thursfield, 1965: 109).

DESCRIPTION. Colonies monosiphonic, up to 50 mm, or polysiphonic up to 300 mm; all sizes branching, the larger colonies branching irregularly, and being limp when out of water. Hydrocaulus variably flexuose, nodal constrictions transverse or sloping in alternate directions. Internodes approximately equal, becoming shorter distally, widely variable in length to breadth ratio between colonies; hydrophore distal, long, usually parallel with internode but sometimes shorter and sloping outwards. Base of hydrotheca usually at approximately 90° to internodal axis although this angle may be greater; hydrotheca very reduced, walls straight, divergent, rim even, not flared; characteristic annulus of perisarc thickening below base of hydrothecal wall, wedge-shaped in optical section (Fig. 11). Hydrothecal renovation frequent, secondary hydrothecae usually forming directly on diaphragm resulting in very short hydrothecal chains (Fig. 11). Hydrocladia inserted

alternately, arising from sides of hydrophores, associated hydrotheca consequently axillary. Hydranth long, 18–25 tentacles (Vervoort, 1941); citron-yellow colour recorded (Storm, 1882) but this perhaps unusual. ♂ gonotheca tubular, slightly curved, aperture terminal; ♀ gonotheca kidney-shaped, with tubular aperture on concave side, similar to that of *H. beanii*, with two projecting hydranths (Billard, 1904; Ralph, 1958).

MEASUREMENTS. See Table 9.

TABLE 9

Halecium sessile. Measurements in μm

	BAY OF BISCAY (1959.9.17.8)	W ENGLISH CHANNEL (1971.7.10.1)	NEW SOUTH WALES (1964.8.7.88)	AZORES (1962.1.15.12)	NEW ZEALAND (Ralph, 1958)
HYDROTHECA					
Length (diaphragm to rim)	25–35	45–55	40–50	25–35	15–20*
Breadth at rim	130–170	160–185	150–170	120–150	c. 125
INTERNODE					
Breadth (min.)	90–130	200	130–170	—	—
Length	550–700	550–650	340–500	—	500–680
♂ GONOTHECA					
Length	980–1035	—	—	—	620–750
Breadth (max.)	185–220	—	—	—	210
♀ GONOTHECA					
Length	—	—	—	—	750
Breadth (max.)	—	—	—	—	400

* Rim to desmocytes ('punctae').

REPRODUCTIVE SEASON. August to end October in NW France (Teissier, 1965; Fey, 1969); possibly also June–July, Cherbourg (Billard, 1904). (The fertile Bay of Biscay material is dated 7 March 1912 in E. T. Browne's hand, but this may simply be the date on which he prepared the slide.)

DISTRIBUTION. Widespread in the North Atlantic including the whole of the British Isles, North Sea and English Channel (Hincks, 1868; Broch, 1918, Kramp, 1935) including the Skagerrak and Kattegat but not the Baltic (Broch, 1928; Kramp, 1935, as *H. articulatum*; Christiansen, 1972). Records are nevertheless scattered. As *H. sessile* the species has been recorded from the Hebrides (Norman, 1867; Hincks, 1868), Dorset and Devon (present material), Denmark (Kramp, 1935) and NW France (Teissier, 1965; Fey, 1969); and as *H. plumosum*, probably indicating records of larger colonies, from Aberdeen (Forbes, 1872), Firth of Forth (Leslie & Herdman, 1881), the Clyde (Chopin, 1894) and 'Ireland' (Hincks, 1868; Duerden, 1897).

HABITAT. Apparently all depths to edge of continental shelf. Recorded on algae and worm-tubes (*Sabellaria* sp.) (Billard, 1904).

REMARKS. This species was last redescribed by Ralph (1958).

The species *Halecium filiforme* Alder, 1862a, is discussed under *H. muricatum* (p. 405).

Halecium plumosum Hincks, 1868, was tentatively identified with the present species by Storm (1882); Christiansen (1972) also commented on the similarity. The present material includes specimens referable to Hincks' description, but in their mode of branching, structure of hydrotheca, manner of hydrothecal renovation and possession of an annular thickening below the diaphragm they resemble specimens referable to *H. sessile* sensu Norman, i.e. smaller colonies. It seems that *H. plumosum* was founded merely on large colonies of the present species and is here regarded conspecific.

Halecium articulatum Clarke, 1875, can be reduced to a synonym of the present species. Of the type material only that from Casco Bay, Maine, could be located (W. D. Hartman, Yale Peabody Museum, pers. comm.). It agrees with *H. sessile* material in having very short chains of hydrothecae, in having the annular thickening below each hydrotheca, in having a hydrotheca axillary to each side-branch, in the shape of the female gonotheca and in general colony habit, so that it appears that the two taxa are conspecific.

Most of the material assigned to *H. articulatum* by Kramp (1935: 150) was examined and similarly found to be identical with *H. sessile*. Apparently the only other European records as *H. articulatum* are those of Jaderholm (1909), Vervoort (1942), Leloup (1952) and Christiansen (1972), respectively from W Sweden, N France, Belgium and Oslofjord. The Belgian material is well described, and is almost certainly *H. sessile*. The W Swedish, French and Oslofjord material, identified from the descriptions of Clarke (1875), Jaderholm (1909) and Kramp (1935), which are here referred to *H. sessile*, are also probably the present species.

Halecium lighti Hargitt, 1924, was referred to the present species by Vervoort (1941) who later, however, accepted the species as valid (Vervoort, 1966). Nutting (1927) had previously doubted its validity.

Halecium tenellum Hincks, 1861

(Fig. 12)

Halecium tenellum Hincks, 1861: 252, pl. 6, figs 1-4; Hincks, 1868: 226-227, pl. 45, figs 1, 1a-c; Broch, 1912: 17-18, fig. 3; Broch, 1918: 46-50, fig. 20 (part); Kramp, 1935: 145-146, fig. 60A; Fraser, 1944: 201-203, pl. 37, fig. 179 (part); Vervoort, 1946: 164-165, fig. 68; Leloup, 1952: 144, fig. 77 (part); Hamond, 1957: 307, fig. 14; Millard, 1957: 193, fig. 5; Vervoort, 1959: 229-231, fig. 8; Naumov, 1960: 454, fig. 344 (syn. *H. geniculatum* Nutting, 1899); Millard, 1966a: 471, fig. 11; Vervoort, 1966: 102, fig. 2; Naumov, 1969: 490-491, fig. 344 (syn. *H. geniculatum* Nutting, 1899).

Halecium geniculatum Nutting, 1899: 744-745, pl. 63, figs 1a-d; [non *H. geniculatum* Norman, 1867 = *H. halecinum* (Linnaeus, 1758)].

Halecium washingtoni Nutting, 1901: 789 (nom. nov. pro *H. geniculatum* Nutting, 1899).

TYPE MATERIAL AND LOCALITY. Syntypes: Salcombe Bay, Devon, England, ♂ colony, on *Cellaria fistulosa* (Linnaeus, 1758) (Bryozoa),¹² in spirit plus three microslides, 1899.5.1.168 (Fig. 12).

¹² Syn. *Salicornaria farciminioides*: Hincks, 1861 (International Commission on Zoological Nomenclature, 1971: Opinion 949).

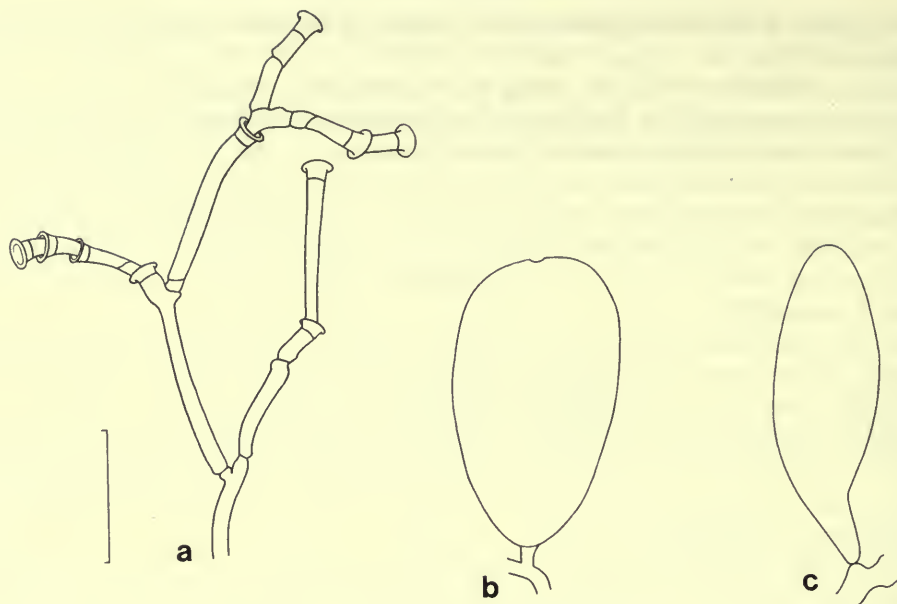


FIG. 12. *Halecium tenellum*. a, part of colony, SW England (syntype, 1899.5.1.168); b, ♀ gonotheca, Republic of South Africa, 46 m (redrawn after Millard, 1966a: fig. 11 E); c, ♂ gonotheca, McMurdo Bay, Antarctica (1964.8.7.90). Scale (a-c) = 500 µm.

OTHER MATERIAL EXAMINED.¹³ Hardanger Fjord, Norway, 200 m, fragments in spirit, coll. A. M. Norman, 1912.12.21.208. Oban, Argyll, Scotland, 1877, several colonies on *Diphasia rosacea* (Linnaeus, 1758), coll. A. M. Norman, 1912.12.21.209. Monte Brazil West, Terceira Island, Azores, 20 m, Aug. 1959, fragments of colonies on sertularian hydroid, coll. Imperial College (University of London) Azores Expedition, 1962.1.15.24. Porto Santo Island, Madeira, 120 m, several colonies on *Eudendrium* sp., in spirit and microslide, coll. R. Kirkpatrick, 1919.8.14.7. Simon's Bay, Simon's Town, Republic of South Africa, 'shallow water', colonies on fragments of type of *Halecium dichotomum* Allman, 1888, two microslides, coll. H.M.S. 'Challenger', 1888.11.13.9B. False Bay, Republic of South Africa, several colonies in spirit, pres. South African Museum, sample of material mentioned by Millard, 1957: 193, station FAL 290C, BM(NH) 1957.4.26.18. Bay to east of Cape Royds, Antarctica, May 1908, 20–40 m, fragments on microslide, coll. Shackleton Antarctic Expedition, 1964.8.7.90 (mentioned, Rees & Thursfield, 1965: 110). Off cable, McMurdo Bay, Antarctica, 17 Feb. 1904, on *Halecium arboreum* Allman, 1888, several colonies in spirit, coll. National Antarctic ('Discovery') Expedition, 1907.8.20.42 (mentioned, Hickson & Gravely, 1907: 28).

DESCRIPTION. Colony erect, up to 20 mm, delicate, monosiphonic, irregularly branched. Hydrocaulus zig-zag in general appearance, internodes usually straight

¹³ This section includes all material of this species in the British Museum (Natural History) collection except the type series.

and narrow, angle between them about 140° . Usually 1-3 annular wrinkles at each end of an internode, but some internodes wrinkled throughout, with intermediate conditions. Hydrotheca borne on prominent distal hydrophore, short, rim flared. ♂ gonotheca pedicellate, ovoid, flattened in one plane; ♀ similar, slightly larger, no protruding hydranths (Millard, 1966a); sexes on separate colonies (Millard).

MEASUREMENTS. See Table 10.

TABLE 10

Halecium tenellum. Measurements in μm unless otherwise stated

	SW ENGLAND (syntypes)	SOUTH AFRICA (Millard, 1966a)	SOUTH AFRICA (Vervoort, 1966)	? U.S.S.R. (Naumov, 1969)
HYDROTHERCA				
Length	25-30	—	30-65	40-80
Breadth at rim	100-130	—	120-135	120-190
HYDROCAULUS DIAMETER (min.)	50	—	—	—
LENGTH OF INTERNODES	500-850	—	875-1300	—
♂ GONOTHECA				
Length	540-720	1070 (max.)	—	—
Maximum breadth	200	600	—	—
♀ GONOTHECA				
Length	—	1070 (max.)	—	—
Maximum breadth	—	510	—	—
MAXIMUM HEIGHT OF COLONY	c. 5 mm	4 mm	—	15-20 mm

REPRODUCTIVE SEASON. Not recorded.

DISTRIBUTION. Poorly known, as many published records are dubious (Hamond, 1957; see Remarks below). British material in the British Museum (Natural History) collection comes from only two localities, Salcombe, Devon (syntypes), and Oban, Argyll. However, the wide distribution suggested by apparently valid published records implies that the species occurs throughout British and nearby waters.

HABITAT. Frequently recorded on other thecate hydroids and on Bryozoa, occurring from sublittoral at least to 495 m (Vervoort, 1966). Recorded on Bryozoa by Hincks (1861, *Cellaria fistulosa*), Hamond (1963, *Bugula plumosa*) and Robins (1969, *Cellaria* sp.). Its apparent association with the hydroid *Idiella pristis* (Lamouroux, 1816) on the West African coast was considered by Vervoort (1959) simply to reflect substrate availability.

REMARKS. The small size and straight, smooth internodes of this species serve to distinguish infertile specimens from young specimens of *H. labrosum*. In addition the curving bases of the hydrocladia in *H. labrosum* contrast with the straighter bases in the present species. Published records should be treated with caution. A summary of records in which the species was confused with *H. labrosum* and its junior synonym *H. undulatum* Billard, 1921, was given by Hamond (1957). See also the Remarks section under *H. labrosum* (p. 398).

Genus *HYDRANTHEA* Hincks, 1868

Atractylis Wright, 1858 : 447 (part) ; Hincks, 1862 : 461.

Hydranthea Hincks, 1868 : 99 [nom. nov. pro *Atractylis* Wright (part)].

TYPE SPECIES. *Hydranthea margarica* (Hincks, 1862), by monotypy.

DIAGNOSIS. Colony hydrorhizal ; hydrotheca pedicellate, borne singly, too short to contain hydranths which are large ; gonophore eumedusoid ; large nematocysts present.

Hydranthea margarica (Hincks, 1862)

(Fig. 13)

Atractylis margarica Hincks, 1862 : 461, pl. 9, figs 4, 4a-e, x ; Hincks, 1863 : 45-46.

Hydranthea margarica : Hincks, 1868 : 100-101, pl. 19, figs 1, 1a-c ; Marine Biological Association, 1957 : 46 ; Huvé, 1954 : 178-182, pls 3-6 (= *Halecium billardii* Kossowska) ; White, 1956 : 39-41 ; Millard & Bouillon, 1973 : 45-46, fig. 6a.

Halecium margaricum : Kossowska, 1911 : 327-328, fig. 1.

Halecium billardii Kossowska, 1911 : 328-331, figs 2-3.

Halecium billardii var. *exiguum* Kossowska, 1911 : 331, fig. 4.

TYPE MATERIAL AND LOCALITY. Ilfracombe, Devon, England, on *Flustra foliacea* (Bryozoa), c. 20 m (Hincks, 1863) ; probably collected summer, 1861 (Hincks, 1862) ; present location unknown.

MATERIAL EXAMINED. Off Sanda Island, Argyll, Scotland, 20-30 m, on *Flustra* sp. (Bryozoa), colony in spirit and two microslides, coll. R. B. Pike, 1955.11.15.11 (mentioned, White, 1956). Off Oxwich Point, Gower Peninsula, Glamorgan, Wales, c. 20 m, 15 Jun. 1971, on *Flustra* sp., colony in spirit, coll. D. N. Huxtable, 1973.3.3.1. Off Poole, Dorset, England, c. 15 m, on *Flustra* sp., colony in spirit, coll. F. Beckford, 1889.7.27.5. Outside Swanage Bay, Dorset, c. 20 m, on *Flustra* sp., colony in spirit, coll. R. Kirkpatrick, 1897.8.9.2. Plymouth, Devon, England, 24 Feb. 1914, colony in spirit, coll. E. T. Browne, 1954.8.3.42. Plymouth, 23 Oct. 1913, fertile colony on *Halecium halecinum*, in spirit and one microslide, coll. E. T. Browne, 1954.8.3.34. Stoke Point, Plymouth, 23 Oct. 1913, colony on fragments of gastropod shell, in spirit, coll. E. T. Browne, 1954.8.3.44. Roscoff, NW France, 12 Sep. 1956, colony on bivalve shell, in spirit, coll. W. J. Rees, 1956.10.24.1-2.

DESCRIPTION. Colony reptant, stolon bearing single hydranths at irregular intervals. Hydranths yellowish-white (Hincks, 1868), on short unringed pedicels, narrow at base, widest just below hypostome, 20-30 tentacles held alternately elevated and depressed (Hincks, 1868 ; Browne, in White, 1956), with small basal web. Hydrotheca short, walls slightly divergent, rim even, diaphragm domed downwards ; c. 20 desmocytes ('punctae'). Large, conspicuous banana-shaped or straight nematocysts (microbasic euryteles, Huvé, 1954), 30-40 μ m long, throughout tissues of hydranth and coenosarc, scattered or in clumps, particularly conspicuous on tentacular web. Gonophores on short pedicel tapering basally, attached to stolon ; gonotheca short (Fig. 13) or absent ; pedicel base said to be enclosed in small chitinous cup (Hincks, 1868) but this not present in all specimens (e.g. BM(NH)

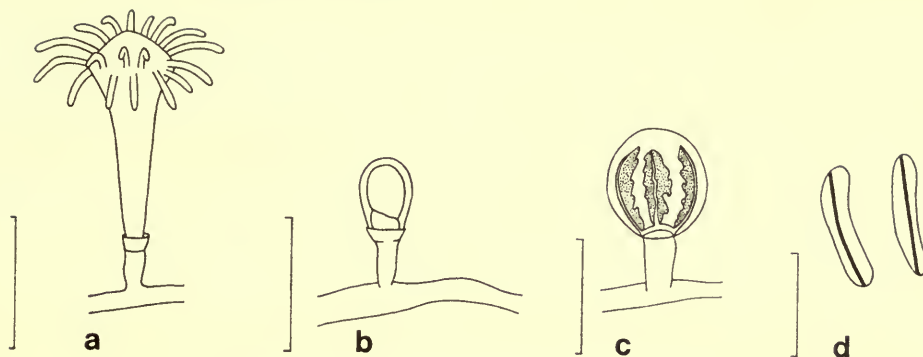


FIG. 13. *Hydranthea margarica*. a, reconstruction of hydranth and hydrotheca, W Scotland, 20–30 m (1955.11.15.11); b, developing gonophore, two-cell stage, SW England (1954.8.3.43); c, mature ♂ eumedusoid, E Mediterranean, lower shore (redrawn after Kossowska, 1911 : fig. 2, as *H. billardii*); d, undischarged nematocysts, SW England (1954.8.3.43). Scales in a–c = 500 μ m; scale in d = 25 μ m.

1954.8.3.43). Fully developed ♂ and ♀ gonophores similar, inverted, medusiform, retained; four branched gastrovascular canals said to be orange in colour. ♂ gametes develop in gonads borne on radial canals; mature ♀ gonophore contains c. 300 ova. (Description of gonophores based on Hincks, 1868, Kossowska, 1911, and Huvé, 1954.) Developing eggs reported in hydrorhiza in a colony apparently lacking gonophores (Millard & Bouillon, 1973).

MEASUREMENTS. See Table II.

TABLE II

Hydranthea margarica. Measurements in μ m

	S WALES (1973.3.3.1)	W SCOTLAND (White, 1956; = 1955.11.15.11)	S FRANCE (Huvé, 1954)
STOLON			
Diameter	60	60–80	90
HYDRANTH			
Height (base to hypostome)	200–400*	400–1000	700
Tentacle length	—	100–170	180
HYDROTHERCA			
Height (diaphragm to rim)	—	—	35
Breadth at base	100	80–90	80
Breadth at rim	100	80–90	100
Hydrothecal pedicel	100	—	150
NEMATOCYSTS			
Length	—	40	30

* Contracted during fixation.

REPRODUCTIVE SEASON. Fertile specimens recorded August (Roscoff, NW France, Teissier, 1965) and October (Plymouth, SW England, White, 1956).

DISTRIBUTION. Recorded from Devon and Dorset, Liverpool Bay, Norfolk and Argyll (White, 1956), mainland Shetland (D. N. Huxtable, pers. comm.), Anglesey (Herdman, 1891), S Wales (present material) and Roscoff, NW France (Teissier, 1965). Elsewhere recorded from the Mediterranean Sea (Kossowska, 1911; Huvé, 1954) and the Seychelles (Millard & Bouillon, 1973).

HABITAT. Most frequently recorded epizoic on *Flustra* spp. and other Bryozoa, but also found on hydroids (*Tubularia* sp. and *Halecium* spp.), mollusc shells and bare rock [Hincks, 1868; Kossowska, 1911; Huvé, 1954; White, 1956; Teissier, 1965; present material (1954.8.3.44.)]; also on *Laminaria* holdfasts (D. N. Huxtable, pers. comm.).

Genus *OPHIODISSA* Stechow, 1919

Ophiodes Hincks, 1866 : 421 [non *Ophiodes* Wagler, 1830 = Reptilia; nec *Ophiodes* Guénée, 1841 = Lepidoptera; nec *Ophiodes* Hartig, 1847 = Hymenoptera; nec *Ophiodes* Murray, 1877 = Arachnida (Marschall, 1873 : 266; Stechow, 1919 : 41; Neave, 1940 : 434)].

Ophiodissa Stechow, 1919 : 41 (part) (nom. nov. pro *Ophiodes* Hincks).

Hydrodendron : Millard, 1957 : 186 (part).

TYPE SPECIES. *Ophiodes mirabilis* Hincks, 1866, by monotypy.

DIAGNOSIS. Haleciidae with long capitate nematophore and short nematotheca; hydranth large; hydrotheca wider than deep, rim even; desmocytes conspicuous; gonotheca barrel-shaped, variably rugose, aperture broad, ♂ = ♀; no medusa generation; large nematocysts present.

REMARKS. This generic diagnosis agrees with the restriction of Vervoort (1959, 1972) in excluding species lacking a nematotheca. Following Vervoort, the one species concerned is retained in the genus *Hydrodendron* Hincks, 1874a; but as noted by Watson (1969) a review of *Ophiodissa* and related genera is needed and present generic limits are somewhat arbitrary.

Ophiodissa mirabilis (Hincks, 1866)

(Fig. 14)

Ophiodes mirabilis Hincks, 1866 : 422–423, pl. 14, figs 1–5; Hincks, 1868 : 231–233, pl. 45, fig. 2; Teissier, 1965 : 20.

Ophiodes caciniiformis Ritchie, 1907 : 500–501, pl. 23, figs 11–12, pl. 24, fig. 1, pl. 25, fig. 5; Babič, 1913 : 473, fig. 7; (syn. nov.).

Ophiodissa mirabilis : Stechow, 1919 : 42; Vervoort, 1959 : 220.

Ophiodissa caciniiformis : Stechow, 1919 : 42; Vervoort, 1959 : 218–221.

Hydrodendron caciniiformis : Millard, 1957 : 186–187, fig. 3; Ralph, 1958 : 342–344, figs 13b–c, 14a; Millard, 1966b : 490–491, fig. 1.

TYPE MATERIAL AND LOCALITY. Holotype : 'on weed', 10–15 m, autumn, 1866, Swanage Bay, Dorset, England; location of material unknown. Neotype : Lower ledges of Capstone, Ilfracombe, Devon, England, lower shore, 1867, infertile colony on four fragments of holdfast of *Laminaria* sp., 1899.5.1.169. The neotype material is labelled '*Ophiodes mirabilis*, Ilfracombe, 1867' in Hincks' hand, and is almost certainly the material he cited later (Hincks, 1868 : 233).

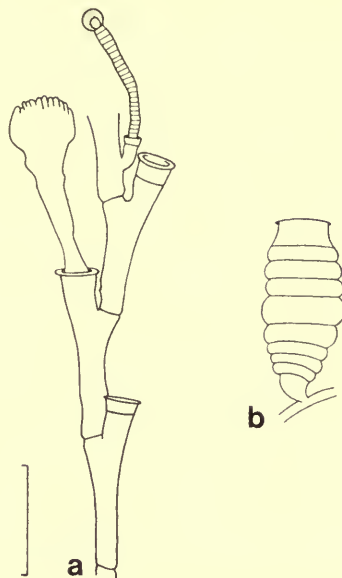


FIG. 14. *Ophiiodissa mirabilis*. a, part of colony with hydranth and nematophore, Cape Verde Islands, 20 m (paralectotype of *O. caciniiformis*, 1964.8.7.92); b, gonotheca, probably SW England (redrawn after Hincks, 1868: pl. 45, fig. 2d). Scale (a) = 500 μ m; (b) unknown.

OTHER MATERIAL EXAMINED. Aran Isles, Galway Bay, Eire, 8 Mar. 1899, colonies on bryozoan, in spirit, coll. E. T. Browne, 1954.8.3.40-41.¹⁴ Freshwater West, near Castlemartin, Pembrokeshire, Wales, lower shore, 15 Sep. 1974, young colony on *Dynamena pumila* (Linnaeus, 1758), microslide, coll. P. F. S. Cornelius, 1974.12.17.1. Porto Praya, Santiago, Cape Verde Islands, 20 m, 12 Aug. 1904, two fragments on microslide, coll. J. Ritchie, 1964.8.7.92, paralectotype of *O. caciniiformis* (mentioned, Rees & Thursfield, 1965). False Bay, Republic of South Africa, infertile colony on alga, in spirit, coll. N. A. H. Millard, 1957.4.26.23 (mentioned, Millard, 1957, as *O. caciniiformis*). Dalebrook, False Bay, Republic of South Africa, LWST, 16 Jan. 1961, infertile colony on brown alga, in spirit, coll. N. A. H. Millard, 1961.6.26.4.

DESCRIPTION. Established colonies irregularly pinnate, loosely polysiphonic basally, up to c. 50 mm but usually less than 20 mm; younger colonies stoloniferous. Hydorrhiza irregularly branched, perisarc thick, with internally-projecting spines; hydrocauli arising erratically. Internodes smooth to slightly wrinkled, hydrophore distal, sloping outwards at c. 45°. Greatest width of hydrotheca c. 1½ times depth; rim even, reflexed; desmocytes conspicuous; annular thickening between desmocytes and diaphragm. New hydrothecae arise from side of hydrophore (Millard,

¹⁴ The material bears the locality 'Aran'. Browne's ms diaries in the British Museum (Natural History) show that on the date given his collectors were in the Aran Isles, Galway Bay, and not the Isle of Aran in Donegal.

TABLE 12
Ophioidissa mirabilis. Measurements in μm

	CAPE VERDE ISLANDS	SOUTH AFRICA (Millard, 1957)	NEW ZEALAND (Ralph, 1958)	SOUTH ATLANTIC (c. 10°49' N, 16°39' W, 42 m; Vervoort, 1959)	SW INDIAN OCEAN (Millard, 1966a)
	(paralectotype of <i>Ophiodes</i> <i>caciniiformis</i>)				
HYDRANTH					
Height (diaphragm to hypostome)	550-700	—	—	—	—
Greatest width	120-170	—	—	—	—
Tentacle length	c. 200	—	—	—	—
Tentacle width	30	—	—	—	—
HYDROTHERCA					
Height (diaphragm to rim)	70-80	85-120	90-120	70-110	—
Width at rim	180-200	210-240	c. 250	—	—
Width at base	120-130	—	—	180-230	—
NEMATOPHORE					
Length	300-800	—	—	—	—
Width	40-50	—	—	—	—
Diameter of terminal knob	80	—	—	—	—
NEMATOTHECA					
Length	120-130	150-200	125-187	130	—
Width at rim	80	10-12	62	90	—
INTERNODE					
Length	350-500	330-540	430-750	350-575	—
Minimum diameter	65-100	—	—	—	—
GONOTHECA ($\delta = \varnothing$)					
Height (max.)	—	—	—	—	1350
Diameter (max.)	—	—	—	—	580

1957; Ralph, 1958). Hydranth large, tapering basally, 18–24 tentacles, held alternately raised and lowered. Nematothecae borne irregularly on internodes, hydrophores and stolon; curved cone-shaped, narrowest basally, sometimes with constriction below rim, both varieties occurring on single colonies; nematophore long, axial cells large, terminal knob with numerous nematocysts including large microbasic mastigophores. Gonothecae apparently recorded only twice. Described as 'ovate, ringed transversely with wide tubular aperture, subpedicellate, borne on stolon', probably ♂ (Hincks, 1866, 1868); similar, but aperture wider, less rugose, ♂ slightly smaller than ♀, no medusa (Millard, 1966b).

MEASUREMENTS. See Table 12.

DISTRIBUTION. Recorded infrequently. From the British Isles, known from Ilfracombe, Devon; Swanage, Dorset (Hincks, 1868; Garstang, 1900); Pembrokeshire (Crothers, 1966; present material) and Aran Isles, Galway Bay (present material). A record from Aberdeen, Scotland (Forbes, 1872), was regarded as dubious by its author. Apparently the only other European record is from Roscoff, NW France (Teissier, 1965). Other records, as *O. caciniiformis*, include the Cape Verde Islands (Ritchie, 1907), South Africa (Millard, 1957), SW Indian Ocean (Millard, 1966b), New Zealand (Ralph, 1958), mid South Atlantic (Vervoort, 1959) and the West Indies (Vervoort, 1968).

HABITAT. Most frequently recorded on algae, particularly laminarian holdfasts, but also on other thecate hydroids. Recorded from *Laminaria* zone of intertidal (Hincks, 1868; present material) down to 65 m (Vervoort, 1959).

REMARKS. *Ophiodissa caciniiformis* (Ritchie, 1907) is here reduced to a synonym of the present species. *O. caciniiformis* was proposed to include colonies larger than those previously referred to *O. mirabilis* by Hincks (1868). *O. mirabilis* has not previously been redescribed; and the larger specimens described by various authors this century have been referred to *O. caciniiformis*. Characters ascribed to *O. caciniiformis* since the original description include an annular thickening of the hydrothecal perisarc below the ring of desmocytes, a goblet-shaped nematotheca and internal projections of the hydrorhizal perisarc (Millard, 1957, 1967; Ralph, 1958; Vervoort, 1959), all of which characters are present in the neotype material of *O. mirabilis*. Further, the paralectotype specimen of *O. caciniiformis* has all the characters of the older species, and the dimensions of the type specimens of the two taxa are similar. It seems that *O. mirabilis* was founded on small colonies, and that larger colonies found later were wrongly given specific status.

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¹⁵ Although dated 1928 this publication was received in the Zoology Library, British Museum (Natural History), on 20 December 1927.

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